AN ANALYSIS OF MORPHOLOGICAL DIFFERENCES AMONG OAKS IN SELECTED MINNESOTA STANDS OF THE *QUERCUS BOREALIS*-*Q. ELLIPSOIDALIS* COMPLEX

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Abstract

The phenotypes of Quercus borealis in northwestern Minnesota grade toward the theoretical phenotypes of Q. ellipsoidalis. The variability could be caused either by hybridization between the two species or by environmental influences. Degree of likeness to a standard species type was obtained from plotting the expression of fifteen morphological characters (from taxonomic manuals and herbarium specimens) on scatter diagrams. The habitat of the stand with the phenotypically most intermediate trees includes a rich soil and a more extreme climate than the other stands. It is the least diverse stand in species composition and has different species from the more temperate stands. The oak trees in it vary significantly from those in other stands in terms of diameter, number of lobes per leaf, percent indentation of leaves, and ratio of inner width to inner depth of acorn cups (by chi-square contingency tests, Bartlett's test for homogeneity of variances, and the Kruskal-Wallis test). The oldest stand is the most diverse and has the individuals closest to the Q. borealis phenotype--either from backcrossing to red oak, because of temperate climate and a history of little disturbance, or a combination of the two.

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Introduction

Northwestern Minnesota is a region of vegetational and climatic transition. Westwards from Itasca State Park, within sixty miles, the vegetation changes from boreal forest through pine-hardwood to savanna and prairie. The climate becomes progressively drier and cooler from Itasca Park towards the prairie to the west (McAndrews, 1966). There is physiographic change along this transect, with resultant local variation in vegetation. Buell and Facey (1960) studied part of this transition, a twenty-two mile transect from the savanna area to the prairie. McAndrews (1966) reported on the vegetation, climate, geology, and postglacial history of the Itasca Transect, a strip sixty-six by six miles from the pine-hardwood forest west into the prairie. The vegetation of the Itasca transect has been well studied, especially in Itasca Park where the University of Minnesota maintains the Itasca Forestry and Biological Station.

In the Itasca Park region the (mixed conifer hardwoods) forest meets the maple-basswood forest, which continues westward (Buell and Gordon, 1945; Buell and Cantlon, 1951). The species of the maple-basswood forest include the red oak, Quercus borealis* as a major species. At the western extreme of the hardwood forest,

*Nomenclature follows Gleason and Cronquist (1963).

in the oak-aspen area, the oaks present are bur oak, Q. macrocarpa, and the northern pin oak, Q. ellipsoidalis. The present study was undertaken to consider the change from the red-oak phenotype to the northern-pin-oak phenotype. The phytosociology of the stands was also investigated to complement the study of the change in morphology of the oaks across the deciduous forest belt of northern Minnesota. The stands were chosen to represent the extremes of the deciduous forest belt (fig. 1). The western stand is in the prairie-forest border area and the eastern stands are near the deciduous-boreal forest border.

The change from the red-oak phenotype to the northern-pin-oak type accompanies the changes in climate, geology, topography, and vegetation. The Itasca transect data do not indicate whether the changes in the oak morphology are due to the environmental changes or are inherent in the genotypes of the trees themselves. The changes in tree structure from east to west can be interpreted as adaptations to a drier habitat (smaller leaves, shorter trees, and smaller acorns are included). These could be genetic traits or environmentally induced. In an attempt to clarify this problem, data from two stands in Cedar Creek Natural History Area are included. These two stands are within a few hundred meters of each other, but manifest many of the differences found

from extreme sides of the deciduous forest portion of the Itasca transect.

The data from each tree in a stand are summarized to permit comparison of stands. The trees within a stand are not completely consistent in their expression of characters and there is overlap of features from trees of one stand with those of the other stands. It is the trees within the stands that vary genetically and that are acted on by the environment not the stands themselves. Since there is some similarity of morphology of trees within stands, however, stands are discussed, as representing an average phenotype of the trees found there.

Hybridization in Oaks

Hybridization among American oaks has been recognized for many years. Many of the early authors were concerned with southern and eastern species. Engelman (1877) described oaks and hybrids of the southwest and south. He commented on the lack of crosses between the black-oak and white-oak groups. Hollick (1888) discussed a single type of black oak, Quercus heterophylla, found on Staten Island. There were few trees similar to it in the area and it was generally accepted to be a hybrid. There was, however, a contemporary disagreement about its possible parents. By comparing leaves with those of local species, Hollick concluded that one parent was Quercus borealis. MacDougal (1907) concurred with Hollick and added Q. phellos as the second parent, based on leaf shape comparisons. Gleason and Conquist (1963) maintained that parentage for Q. heterophylla. MacDougal made many observations of plants hybridizing in their native habitat. He was one of the first to emphasize the nonequivalency of reciprocal crosses. He also stated that frequently hybrids form a genocline between the parent species. The characters of the individuals of the F_1 generation are usually intermediate between the parents: the characters of individuals of the F_2 generation range through intermediate from similarity to one parent to similarity to the other. The idea of a

genocline between the parental species was later expanded by Anderson (1949) in his discussion of introgressive hybridization.

Ness (1918, 1927) performed experiments on cross pollination with several Texas species of white oaks (Quercus lyrata x virginiana and Q. minor x virginiana). Fertile offspring were produced in the F_1 and F_2 generations of both crosses. The original F_1 hybrids had leaves intermediate in shape between the leaves of the parents. The F_2 hybrids had leaves whose shapes varied widely among the trees. Other crosses occurred naturally and by artificial pollination. All the F_1 and F_2 hybrids produced seeds of normal viability.

Yarnell (1933) continued the work Ness had begun on the Q. lyrata - Q. virginiana F_2 crosses. In studying the characteristics of the F_2 hybrids, Yarnell found a strong tendency for the F_2 hybrids to have the characteristics of one parent species, rather than a mixture of characters. He assumed that there is segregation in the F_2 generation and that factors of one species influence the expression of characters normally found in the other. The F_1 were uniformly intermediate between the parental species.

In his monograph, The American Oaks, Trelease (1924) emphasized southern and Mexican oaks. He discussed the biennial fruit maturation of the black oaks,

subgenus Erythrobalanus, that causes the black oaks to be incompatible with the white oaks, subgenus Lepidobalanus. Trelease listed 51 known hybrids among the US oaks, saying they are usually intermediate in character between the parents. Hybridization is always within a subgenus.

In 1932 Allard reported on probable oak hybrids in the area of Washington, D.C. He never encountered an area with abundant hybrids, although he found and described several natural hybrids. All the crosses Allard described were within one or the other of the subgenera.

Palmer (1942) discussed the red-oak complex, a group of species in the subgenus Erythrobalanus, and considered them all interfertile, but he did not discuss the hybrids. In 1948 he reviewed the history of studies of oak hybrids in the United States. He was discussing hybrids, but he stressed that non-hybrid aberration often occurs. Since leaves are often used as indicators of hybridization, he listed several ways in which abnormal leaves could occur: among these are juvenile growth, second growth after defoliation, and adventitious shoots. The aberrant characteristic would occur throughout the a hybrid, not just on an affected branch. Palmer considered the fruits to be less variable than the leaves in many species and therefore a better character for studies of hybrid oaks. Muller (1941) had made similar observations on leaf variability, and

included stump sprouting, ecological stress, and heterozygosity from ancient crosses as causes of variability.

Pjatnitsky (1946) experimented on oaks by artificially crossing various species. His experiments were aimed at species taxonomically and geographically removed from one another, which included crossing European and American species. Most of the crosses produced viable offspring with mixed morphological characters: an exception was crosses involving Q. borealis, which produced few acorns. None of the other species in these exceptional experiments belonged to Erythrobalanus, which provided experimental basis for the field observations that the subgenera do not cross.

Stebbins, Matzke, and Epling (1947) studied oaks from an area where the ranges of Q. marilandica and Q. ilicifolia overlap. When the trees from the study area were compared with trees from populations of each species outside the overlap area, the characters compared showed evidence of introgressive hybridization.

Cooperrider (1957) used graphic analysis to describe introgression between Q. marilandica and Q. velutina in Iowa.

Much work has been done on natural hybridization of oaks in the southwestern United States. Muller (1952)

found intermediate forms of a complex of crosses only in intermediate habitats. The species he studied each have different, specific soil requirements, a result of which is a strong correlation between the kind of soil and the amount of hybridization in the stands. Intermediates grow only where the two soils occur together. He proposed that other crosses have fewer hybrids surviving, because of lack of suitable intermediate habitat.

Cottam, Tucker, and Drobnick (1959) investigated some clones of apparent Q. gambelii x turbinella hybrids to aid in determining past climatic history of the southwest. In regions where the proposed parents meet, there are new and ancient hybrid clones found in ecotonal areas; Q. turbinella is of semi-arid chaparral and Q. gambelii is of cooler areas. Ancient clones are also found in areas where the chaparral species is not found. The presence of the hybrid clones was used to hypothesize a drier, warmer climate in the past that would have allowed joint occurrence of the parental species in the region currently occupied by the hybrids. The area is mountainous, which would have allowed the parental species to be close to each other while in their own preferred environment on different slopes.

Tucker (1961, 1963, 1970) discussed the Q. undulata complex of the southwest, of which Q. gambelii and Q.

turbinella are a part. This southwestern complex of oaks is similar to the red-oak complex of the north. Because of continuing influx of genes from several species, the separation of species is difficult in both areas.

Other natural populations of oak hybrids have been studied in depth. Q. bicolor x macrocarpa in Ithaca, New York, was complicated by additional crosses with Q. alba (Burger, 1959). Q. alba and Q. montana cross near Chapel Hill, North Carolina, producing hybrids that occur on disturbed ground (Silliman and Leisner, 1958). There, in a stand of suspected hybrids, approximately 35% showed hybrid nature from vegetational characteristics. Some vegetational characters were plotted in a hybrid index of the sort proposed by Anderson (1949). A few of the suspected hybrids, probably the F_1 hybrids, were intermediate between the hypothesized parental types, but most trees, probably the F_2 generation or its derivatives, were closer to one parent than the other. The vegetational characters used were leaf characters and length of the terminal bud. That study concluded that sun leaves were the most characteristic of a tree, the leaves there being assumed to be least variable. That observation has been made repeatedly (Burger, 1959; Morley, personal communication).

European oaks also hybridize. Cousens (1963,

1965) has studied the crosses between two species of the British Isles and the continent. He used scatter diagrams of the type proposed by Anderson and concluded that Q. petraea and Q. robur display introgressive hybridization over most of their range.

Because of the longevity of oak trees, Stebbins (1950) considered them to form fairly closed communities, a situation which would result in hybrids being isolated. The isolation could facilitate backcrosses to a dominant parent, rather than to other hybrids. Palmer (1948) also used an argument involving rare plants to explain the relative scarcity of hybrids in nature. Any one acorn produced by any tree has very little chance of survival. In a mature forest where a pure type of oak predominated, that type would produce most of the oak pollen in the forest and would therefore be likely to fertilize most of the oak flowers in the forest. So, the parental type, or a backcross to it, would be the most likely genotype for most of the few acorns that survive to become mature trees.

The various studies of hybridization in nature have generally stressed the intermediacy of the habitat of hybrids. Thus, the above argument of rarity of hybrids in a mature forest appears to fit for stands that have not encountered large-scale openings. It may not apply as well where new habitats are opened

or where both parent types are present and a catastrophe abruptly opens areas for invasion by available seed crop.

Itasca Transect

Vegetation:

From Itasca Park west to the crest of the Big Stone Moraine, McAndrews (1966) recognized several vegetation types: pine-hardwoods (mixed pine-hardwoods and Pinus strobus-hard-woods) and mesic deciduous (maple-basswood, elm-basswood, and oak-aspen) (Fig. 2). Farther west are regions of oak savanna and prairie. Buell and Facey (1960) classified the natural vegetation in the same transect as maple-basswood forest, oak and oak-aspen groves, aspen stands, shrub communities, marshland, and dry, mesic, and wet prairies. They reported that most of the vegetation borders were gradual, but the maple-basswood forest ended abruptly on the Big Stone Moraine. Much of the area of the transect is now under cultivation which provides some difficulty in ascertaining the natural vegetation and its limits. Janssen (1967) had to use woodlots as representative of forests on the Big Stone Moraine.

Buell and Facey and McAndrews stressed the importance of microclimate produced by the physiography of the morainic area: relief affects precipitation and temperature, and lakes provide fire breaks, especially important in presettlement times. Soils on sandy outwash tend to support xeric communities of Pinus banksiana or Quercus macrocarpa and Q. ellipsoidalis, whereas

soils on till of finer texture support mesic communities of Tilia, Acer, Ostrya, Quercus borealis, Ulmus, and Populus grandidentata.

The oak and oak-aspen groves Buell and Facey described are characteristic of the Big Stone Moraine. They occur most characteristically as a mixture of bur oak, northern pin oak, and aspen. Unless grazed, they usually have a dense shrub layer and trees with low spreading branches. Typical shrubs are Cornus alternifolia, C. racemosa, Corylus americana, C. cornuta, Prunus, Ribes, Rhus, Symphoricarpos, and Viburnum.

The areas of the present study are in T. 142 and 143 N., R. 36 and 40 W. From the bearing trees of the Government land survey of 1871, McAndrews was able to identify the vegetation at that time. R. 34-39 W. were in the pine-hardwood forest, with R. 40 being the western limit of the pines. R. 41 was of the oak-savanna type. R. 39 and the eastern third of R. 40 were burned at the time of the survey. McAndrews speculated that if left alone these areas would have grown to prairie and oak-savanna at the low altitudes and elm-basswood or maple-basswood at the higher elevations.

Geology:

McAndrews (1966) reported on the geology of the Itasca transect. The easternmost part, in Hubbard and Clearwater Counties, is on the Itasca Moraine, with

sandy till from the Wadena Lobe of the Wisconsinan glaciation: on this developed a calcarious sandy-loam soil. R. 40 is on the Big Stone Moraine, which is composed of silty till from the Des Moines Lobe and on which a calcarious silt-loam soil developed. The Big Stone Moraine was formed after the Itasca Moraine and is lower than the Itasca Moraine (Fig. 2). Proceeding west from the Big Stone Moraine are: ground moraine, the Erskine Moraine, and the beaches of Glacial Lake Agassiz in R. 44, 24 miles west of the crest of the Big Stone Moraine. The gradual rise from west to east has an influence on the climate of the transect; the east receives more precipitation. The whole area has probably been deglaciated for 12,000 years, with some areas open for vegetation invasion for 13,500 years.

Climate:

Kell (1938) considered the mean precipitation of Itasca park (60.1 cm/year) to be similar to that of the prairie to the west. She believed that the differences in vegetation result from the less droughty soils in the park area that could support mesic forest. McAndrews (1966) reported greater and more persistent snow cover in the forest area than in the prairie-forest transition. On the prairie and in the ecotone, the weather is more variable than in the forest, with a greater risk of a deficit of summer rainfall. The ecotone is between the

area of influence of tropical air masses that affect the forest and the area of dry interior air which affects the prairie. McAndrews postulated that the climate of the transition zone is in constant flux; depending on which air mass dominated in a given year, the ecotone would be moist or droughty. He suggested that a small increase in temperature accompanied by a slight decrease in rainfall would cause the vegetation of the ecotone to become prairie-like, but the forest would be able to dominate were snow cover to increase and winter temperature to decrease.

Buell and Wilbur (1948) reported that Mahnomen County, on the Big Stone Moraine, is more xeric than Itasca Park, the latter having more snow cover and a greater maximum temperature, except in late summer. They and the others who discussed the climate of the transect concluded that the climate of the prairie margin is more extreme than the climate in Itasca Park.

Figure 2. Section of the Itasca Transect

a. topography and soil parent material

b. location of stands in this and previous studies, with vegetation formations.

Key to b.

1 = Mixed pine-hardwood

2 = Pinus strobus-hardwood

3 = Acer-Tilia type forest

4 = Ulmus-Tilia type forest

5 = Quercus-Populus type forest

6 = oak savanna

7 = prairie

J - relevé by Janssen (1967)

R - Reichow Stand, McAndrews (1966)

W - Waubun Stand, Buell and Cantlon, (1951)

M - Stand M

Z - Stand Z

A - Stand A

Methods

In the Itasca transect I chose three forest stands for the study. Requirements to be met in choosing stands were accessibility and a plenitude of oaks. The stands were found primarily from advice of faculty and students of the Itasca Biology Station who were familiar with the area.

Stands A and Z are located in Itasca Park, within the SE 1/4 NW 1/4 SW 1/4 sec. 24, T. 143 N., R. 36 W. and the NE 1/4 NE 1/4 NE 1/4 sec. 5, T. 142 N., R. 36 W., respectively. Stand M is located in Mahnomen County in the NW 1/4 NE 1/4 NW 1/4 sec. 5, T. 143 N., R. 40 W.

Within each stand twenty oak trees of the Erythrobalanus subgenus--red oak or northern pin oak in northern Minnesota--were chosen. In the field, each tree was scored on fifteen characteristics describing the tree including tree, branch, and bark appearance, and acorn type. Acorns were gathered from the ground beneath the trees and were assumed to be from the tree directly above; squirrel caches were not used for this purpose. As many acorns as possible were obtained, many from past years. In many cases the cups were much more common than entire acorns, one of the several indications of squirrel activity in the stands. Other signs were collections of acorns in the duff, disturbance

of the litter layer, and new acorns cut from the trees. The inner depth and inner width (fig. 2a) of the cups were measured to the nearest tenth millimeter for the ratio between them. Leaves were clipped from each tree, generally the lowest leaves on the tree. These were cut with an extendable pruner. No attempt was made to obtain leaves from a particular direction or from different branches, as often only one branch was within the twenty-five-foot reach of the clippers. Thirty leaves per tree were collected and scored for texture, base angle, and color. The number of lobes was counted, including any tip directly connected to the midrib by a vein. Per cent indentation above the largest lobe was also obtained (fig. 2b). Only leaves on which all measurements and observations could be made were used. Many leaves had to be rejected because of insect damage. For each tree the height was approximated with an Abney level, the dbh in inches was measured, and the age at one-meter height was obtained using a Swedish increment borer.

Each oak was used as the center for a point-quarter sample of the stand. For each point-quarter-tree, species, dbh, and distance from the center tree were recorded. From a transect one meter wide from the center tree to each point-quarter tree, the number of seedlings and saplings, and the percent cover of shrub layer species

Figure 3. Methods of measuring quantitative characters

a. acorn cup measurement

i. whole acorn cup

ii. cross section of an acorn cup

ratio = inner width/inner depth

b. leaf characters 3/4 size

base type - rounded

Number of lobes = II

% indentation: A and B were measured

C, from subtraction (A - B = C)

= C/A X 100

Mean results from the U of M herbarium are listed in Appendix D

were recorded. The actual area sampled per stand varied with the density of the stand.

For the part of the study dealing with the morphology of the oaks, trees at Cedar Creek Natural History Area in Anoka County were also studied, also chosen from stands considered to be reasonably representative of one or the other oaks by workers familiar with the area. This work was done as a preliminary to the Itasca study. Two stands were chosen: Crone's Knoll, a mesic area, and the edge of a nearby field. These trees were scored on characters similar to those used in the Itasca transect. Several spring features were also scored at Cedar Creek. No heights or ages were obtained.

Phenology of flowering was followed at Cedar Creek in the spring of 1971. Pollen from the eight trees at the edge of the meadow, the only ones where it was accessible, were tested for viability using a general protoplasmic stain, aniline blue in lactophenol (Sass, 1940). Unstained grains were counted as inviable.

The Botany Herbarium and several taxonomic manuals were used to obtain standard species types. It must be stressed that for all leaf comparisons the standard types are from herbarium specimens from Minnesota only. According to Dr. John Moore (personal communication) the northern pin oak in the herbarium probably includes hybrids with red oak, although the red oak is fairly pure. Three leaves from fifty trees

of each kind were used from the herbarium. The number of lobes was counted and the percent indentation above the largest lobe was obtained on each leaf, then averaged for all leaves of a specimen. No specimen that had been identified as anything other than the one of interest was included.

Description of Stands

Stand A, located south of Lake Itasca in Itasca Park, is the easternmost stand. It is in Janssen's (1967) Tilio-Acerion sacchari alliance. The soil has a layer of humus, a thin dark A_1 horizon, a lighter A_2, and a light brown, somewhat clayey B horizon. The parent material was deposited by the Wadena Lobe.

Stand A is the most diverse of the three stands, with nine species of trees in the sampled area, but it is the least dense, with 6×10^2 trees per hectare. The basal area is 29 m^2 per hectare. Stand A has 4.9×10^4 seedlings per hectare, about three times the density of the other stands. Of the twelve species of seedlings in A, all but three species are the same as the tree species of the stand. There are five species of saplings, all of which occur as trees also. Stand A has the lowest density of saplings of all the stands, with 4×10^2 per hectare. No one species of sapling was represented by far greater numbers of individuals than the others in the sample area. There were three species with three individuals each and two other species with two individuals each. The shrub layer contains fewer species than either of the other stands, and covers less of the sampled area. Appendix A contains details about this and the other stands.

Stand A has the tallest and oldest individuals

and greatest mean height and age of any of the oak trees sampled. The area was burned repeatedly in the 1800s: 1803, 1811, and 1875 (Frissell, 1971), but it has been protected from fire since the 1920's. There are several red pine trees in the stand, each with multiple fire scars, probably dating from the 1800s. Other tree species in the stand are not fire tolerant, indicating establishment of the present forest since the last major fire in 1875.

Stand Z is about four miles southwest of stand A and is also in Itasca Park. It was in a two-mile-wide area in the western part of the park that was clear-cut and burned between 1900 and 1920 (Frissell, 1971). The oak trees are the youngest for any stand, with a mean age of 48 years at waist height (about one meter). The oaks form a subcanopy with a mean height of 18 meters, under a Populus tremuloides-P. grandidentata overstory. This stand is the densest of the three investigated, with 7.4×10^2 trees/ha. Since the three stands have quite similar basal areas per hectare, stand Z has the lowest mean basal area per tree.

Six species occur as trees in the samples at Z; twelve species, including all the tree species, are found as seedlings; and six species, four the same as the tree layer, occur as saplings. Acer rubrum occurs far more often than any other sapling species. This disparity in the constitution of age classes probably

results from the immaturity of the canopy and subcanopy layers, which indicates future changes in composition of the forest. The Populus species were not represented by saplings, and although seedling-size stems are present, especially of P. tremuloides, they may be root suckers able to survive because they are connected to the parent tree. A survey of the woods revealed only one species of tree not included in the sample: a single Picea glauca individual was recorded. This site is several miles west of the main mixed coniferous-deciduous forest border that Buell and Gordon (1945) studied, which suggests that the spruce might have been a chance immigrant when the area was open for invasion. Or it might be a surviving representative of the pre-logging forest that was left by the timbermen. The shrub layer in Z had 18 species, more than in either other stand.

The soil at Z was derived from Wadena Lobe drift. It has a humus layer of variable depth, an A_1 horizon of 1 to 2 inches, an A_2 about 2 inches thick, and a browner, very fine B. The soil had very little clay in it. The soil pit was dug on the same day as the pit at stand A and appeared to be a bit moister than at A; the clods stuck together better at Z.

Several studies preceded the present one in the prairie-forest tension zone. Buell and Cantlon (1951) studied the Waubun stand at the western limit of the

hardwoods in sec. 17, T. 143 N., R. 40 W. They found a degraded chernozem soil and trees dating from 1810. They hypothesized a change in burning pattern and climate that allowed the forest species to invade the prairie area. That stand had no open-grown trees. Shontz and Baker (1962) studied a bur oak stand in sec. 33, T. 143 N., R. 41 W. They also found a degraded prairie soil. There were large open-grown bur oak in the stand, surrounded by younger trees dating from around 1900 when regular burning of the area ceased.

Stand M is in Mahnomen County, twenty-six miles west of stand Z on the west slope of the Big Stone Moraine. The soil appears to be a degraded prairie or savanna soil: up to an inch of litter, 1 inch of humus, 1.5 inches of a very black layer, 4.5 inches of dark brown-gray horizon, and a brown layer below. It was dry below the humus. Throughout the stand are several large individual bur oaks with large, low spreading branches, which indicate open conditions when the trees were becoming established. McAndrews (1966) reported that the federal land survey of 1871 found R. 40 W. burned over, which allowed new communities to become established: prairie and oak savanna at low altitudes and Ulmus-Tilia or Acer-Tilia forests at higher altitudes. Older residents of the region

told Buell and Facey (1960) that until white settlement in 1905 fires were common. Before that time the region of stand M was probably maintained as an oak savanna by the fires. Bur oak has thick bark that makes it resistant to most ground fires. With the removal of fire the less resistant or nonadapted species were able to become established. Shontz and Baker (1964) attributed the presence of a few scattered bur oaks in their study area to forest encroaching on savanna, an interpretation I feel would be safe to apply to stand M.

The trees of northern pin oak-type in stand M have a mean age of 52 years. The ages range from 32 to 67 years. This range indicates a possible continuing immigration for 35 years into a somewhat open forest, since neither red oak nor northern pin oak is particularly shade tolerant.

The process of invasion appears to be continuing. A few mesic-forest species, notably Acer rubrum and Tilia americana, are found only as seedlings in the stand. The seed source for these species is near by; Janssen, McAndrews, and Buell and Cantlon all reported the area to be at the edge of, and within, the hardwood forest. Sapling (1" to 3.9" dbh) data are not as indicative of change as the seedling data: bur oak (11 individuals) and northern pin oak-type (2 indivi-

duals) were the only species represented by more than a single individual, and aspen and elm each had one individual present. This would indicate only a slight change of composition for the next generation of trees.

The trees in stand M are of five species with 6.5×10^2 trees per hectare. This is quite similar to the results McAndrews (1966) reported for two nearby stands, the Reichow and Waubun stands. The species present in M vary from the species at those stands. There are only three coincident species: Populus tremuloides (with density and basal area similar for M and the Reichow stands, it was absent from the Waubun stand), Ulmus americana (densities and dominance similar in all three stands), and Quercus macrocarpa (much greater density and dominance in M) (Table 1).

Table 1. Comparison of three prairie-forest border stands

	Density trees/ha			Dominance m^2/ha		
	R	W	M	R	W	M
Acer saccharum	335.6	332.3		10.7	13.0	
Betula papyrifera	40.0	50.4		.9	2.2	
Fraxinus nigra	25.5			1.0		
F. pensylvanica	20.0	4.0		.4	.1	
Ostrya virginiana	30.1	59.3		.3	1.0	
Populus balsamifera	4.9	35.6		.6	1.2	
P. tremuloides	139.9		105.6	4.5		4.4

	Density trees/ha			Dominance m^2/ha		
	R	W	M	R	W	M
Prunus serotina			16.3			.6
Quercus borealis-type			219.8			17.0
Q. macrocarpa	10.1	19.8	260.0	.5	.7	11.1
Tilia americana	120.0	90.9		10.9	7.5	
Ulmus sp.	50.4	47.4	48.8	5.2	5.7	1.4
Totals	776.6	639.7	650.0	35.0	31.5	34.4

R = Reichow stand
W = Waubun stand
M = stand M

After McAndrews 1966.

The densities from the stands of the present study are not accurate. They could underestimate the actual density since a tree is used as the center and is not included in the calculations. Or, if the trees are aggregated, the result of such sampling could overestimate the density. The center trees are not a random selection, but were chosen as mature trees, which would further reduce the density reported from the actual density. For comparison among stands A, Z, and M the errors may be less important, because their densities were all calculated the same way. Since the oak trees are different from one stand to another, another expression of the difference could be the degree of aggregation, which would change the estimate of density from stand to stand. Such change in aggregation

could be genetic or environmentally induced. For all comparisons involving density the numbers should be considered as approximations.

Results of analysis:

Several methods of comparing stands were used: these were based on importance values of trees from the point-quarter method; relative density of seedlings and saplings; relative cover of shrub layer species; and mean age, dbh, and height of the oak point trees in each stand.

$$D_{jk} = \sqrt{\sum_{n=1}^{m} (X_{ij} - X_{ik})^2}$$

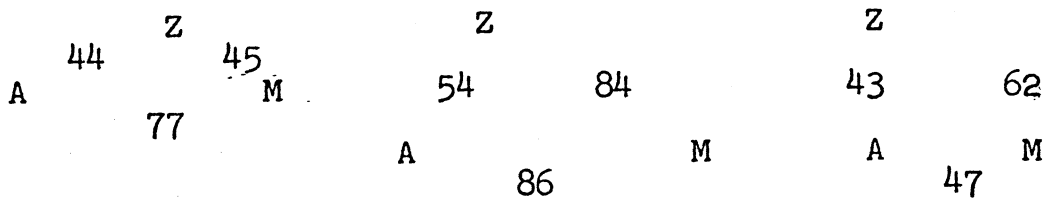
D_{jk} = distance between stands j and k
X_{ij} = a measure of species
m = number of species in the two stands being compared, j and k

The above index of dissimilarity was used to interpret the differences between stands. It is a method of ordination in which the species define orthogonal axes and the stands are plotted as points in the resultant multidimensional space. If the stands were identical, D_{jk} would be zero. The further the results are from zero, the more dissimilar are the stands being compared. Table 2 summarizes the results.

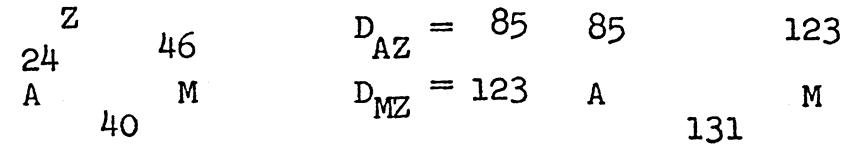
Table 2.

Dissimilarity coefficients

Seedlings:	Sapplings:	Trees:
$D_{AM} = 77$	$D_{AM} = 86$	$D_{AM} = 47$
$D_{AZ} = 44$	$D_{AZ} = 54$	$D_{AZ} = 43$
$D_{MZ} = 45$	$D_{MZ} = 84$	$D_{MZ} = 62$



Shrub layer:	Totals:
$D_{AM} = 40$	$D_{AM} = 131$
$D_{AZ} = 24$	$D_{AZ} = 85$
$D_{MZ} = 46$	$D_{MZ} = 123$



In every case the data compared are relative figures. The seedlings and sapling data are in relative density per stand and the shrub layer is in relative cover per stand. The importance values (IV) of trees is the sum (relative density + relative dominance + relative frequency)/3, calculated for each species in a stand. The totals, above, are the sums of the values for the seedling, sapling, tree, and shrub layers.

$$\text{Total } D_{jk} = \sqrt{\text{Seedling}^2 + \text{Sapling}^2 + \text{Trees}^2 + \text{Shrub}^2}$$

The statistics for each stand are in appendix A.

Discussion:

Stand A is the most diverse stand in tree species, and the least dense. The seedlings in A are the most dense; the saplings are the least dense. All layers share species which indicates a forest reproducing itself with great seed production. Only a few of the new individuals will survive the shading of the full canopy. The shrub layer is the sparsest of any stand, which also indicates a full, closed canopy. The oaks are tallest and oldest in stand A. The forest has not been burned since 1875, nor was it logged at all, allowing a deciduous forest to become established; it is apparently a steady-state forest.

The dissimilarity coefficient indicates A is the most consistently like Z for all parameters. The similarity is quite reasonable in light of the proximity of the stands to one another and similarity of their soils. The history of the stands is different, as demonstrated in Z by the dissimilarity of species in the tree, sapling, and seedling classes. Z was cleared, which allowed a possible large-scale invasion of disseminules of all nearby species by then existing adults although there was probably regeneration from stump sprouting. In the case of the oaks, some of the available acorns would have had a chance to grow, which would increase the probability of a variety of genetic

combinations becoming established.

There was a subcanopy of deciduous-forest trees under the canopy of aspen in Z. The oaks are youngest in Z. The sapling and seedling classes are more indicative of climax forest than is the tree layer: Acer, Ostrya, and Quercus borealis-type are strongly represented in those two age classes. The shrub layer in Z is the most dense, a result of the openness of the canopy layers. Most of the eighteen species of the shrub layer are shared with either A or M. Corylus cornuta is the dominant shrub species of A and Z, and also occurs in M. The shrub layer in Z may be left over from the logging days of the area. Corylus, for example, reproduces through sprouting, and fire often leaves it undisturbed (Buckman, 1964). The dense layer is in competition for light and space with the seedling class and has been with the sapling class. This competition would reinforce selection for the shade-tolerant species of the mature forest.

Seedlings are an indication of future directions of the stand, as well as being representative of the current seed and sprout production. Only in seedling size composition is Z at all similar to M. The similarity between M and Z in the seedling size class is strongest in Populus, Prunus, and Amelanchier, all in large numbers in each stand. Populus root-sprouts

and is not an indicator of the future once the parent trees are gone. The other two genera are opportunists that seldom become dominant in Minnesota forests. Thus, the future composition of stands Z and M is less likely to be similar than the seedling data indicate.

Stand M is fairly consistently unlike either other stand. In trees, it is as similar to A as Z is, but M is also dissimilar to Z. In seedlings, as discussed above, M is somewhat similar to Z, but dissimilar to A. In saplings and the shrub layer, M is about equally dissimilar to A and Z. Stand M is the only stand to have Corylus americana in its shrub layer; it constituted 16% of the shrub cover in stand M. C. americana tends to grow in more xeric conditions than C. cornuta (Buckman, 1964), an observation that correlates with the reports of drier climate in the western part of the transect. The soil is not droughty at M, but is a rich prairie soil that could support a vigorous vegetation if other conditions were appropriate. Climatic conditions in the tension zone are more extreme than to the east. Fewer species of trees are able to survive these conditions than those in the east.

Stand M is an example of an area that was opened for invasion of fire-intolerant species in the early 1900s, when regular burning of the area was halted.

The rich soil and limited precipitation of the area around M combine to form an intermediate habitat for which a hybrid might be better suited than a species adapted for the greater moisture of the deciduous forest (red oak) or one suited to droughty soils (northern pin oak).

Cottam (1949) studied Stewart's Woods in southwestern Wisconsin. It was an oak opening in the 1830s, but it had become an oak woods by 1949, where it had not been disturbed. The climatic conditions are more suited to tree growth there than in western Minnesota: Wisconsin has a longer growing season and greater precipitation. Still, the prairie-forest border woods are quite similar. Cottam found that oaks dominated the stand: bur oak was the most common tree, as it is in stand M of the present study. In Stewart's Woods, bur oak was present only in the larger size classes. Other oaks, Q. alba and a complex of black oaks (Q. velutina, Q. borealis, Q. ellipsoidalis, and their hybrids) made up the smaller sizes. There were fewer oaks than expected in the sapling class, except in exposed areas. The future of Stewart's Woods, as represented by the younger age class, was as an Acer-Tilia-Ulmus forest. In 1949, the woods had a density ten times greater than when the land was surveyed. There also, the influence of settlement was to decrease the fires that had maintained oak savanna between the prairie and forest.

There appears to be a consistent vegetation pattern in a prairie-forest tension zone. Curtis (1959) characterized the dry southern hardwood community as one dominated by oaks with a 50-90% canopy. This fits the general description of the tension zone from Minnesota to the prairie peninsula through Illinois (Kilburn, 1959; Geis and Boggess, 1970) and includes oak openings in Oregon (Thilenius, 1968).

In the present study some of the oak-tree data indicate similarities and differences of the stands. Graphing the ages against the diameters of the main trunks (fig. 4a) indicates some correlation between them. Linear regression and correlation coefficients for these data would not be very accurate as the diameters from stand to stand do not have homogeneous variances. (Results of Bartlett's test for homogeneity of variances are in appendix C.) There is no significant difference in total basal areas per stand (appendix C). The disparity between basal area and dbh data is probably due to the prevalance of multi-trunked individuals in the stands. All trunks were used in calculating dominance, but only one was used for the dbhs. The causative factors of the multiple trunks are in the history of the stands: perhaps M was heavily browsed when the trees were young; there may have been frost damage to the leading stems in A; an older trunk in Z may have been

cut and the present trees are sprouts from its stump. It is possible that multiple trunks may be genetically controlled; the ability to recover from damage certainly is, and may vary with the species. Since the trees studied were the ones that survived, and the ones that did not are not available for comparison, this particular avenue of species comparison is closed.

When age is graphed against height of the tree (fig. 4b) there is no apparent overall correlation. The data for each stand by itself are indicative of a within stand age-height correlation. These results suggest that the smaller size of the trees at the prairie-forest border (M) are not due to younger age, but rather to local growing conditions, heredity, or both. Daubenmire (1936) also reported shorter trees as the prairie was approached, which indicates that stand M is not unusual in that respect.

Figure 4. Tree distribution for correlating growth parameters

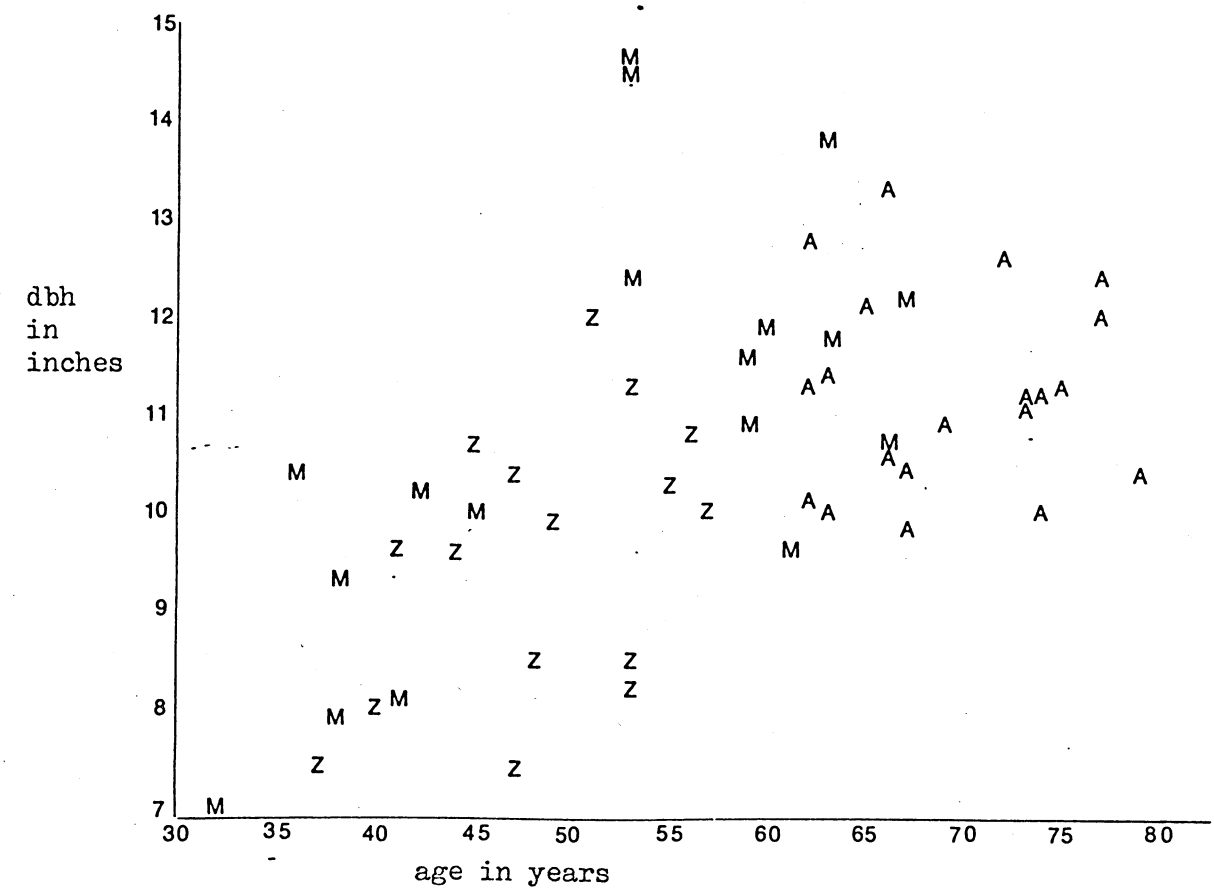
a. diameter vs. age

b. height vs. age

A = 1 tree from stand A

Z = 1 tree from stand Z

M = 1 tree from stand M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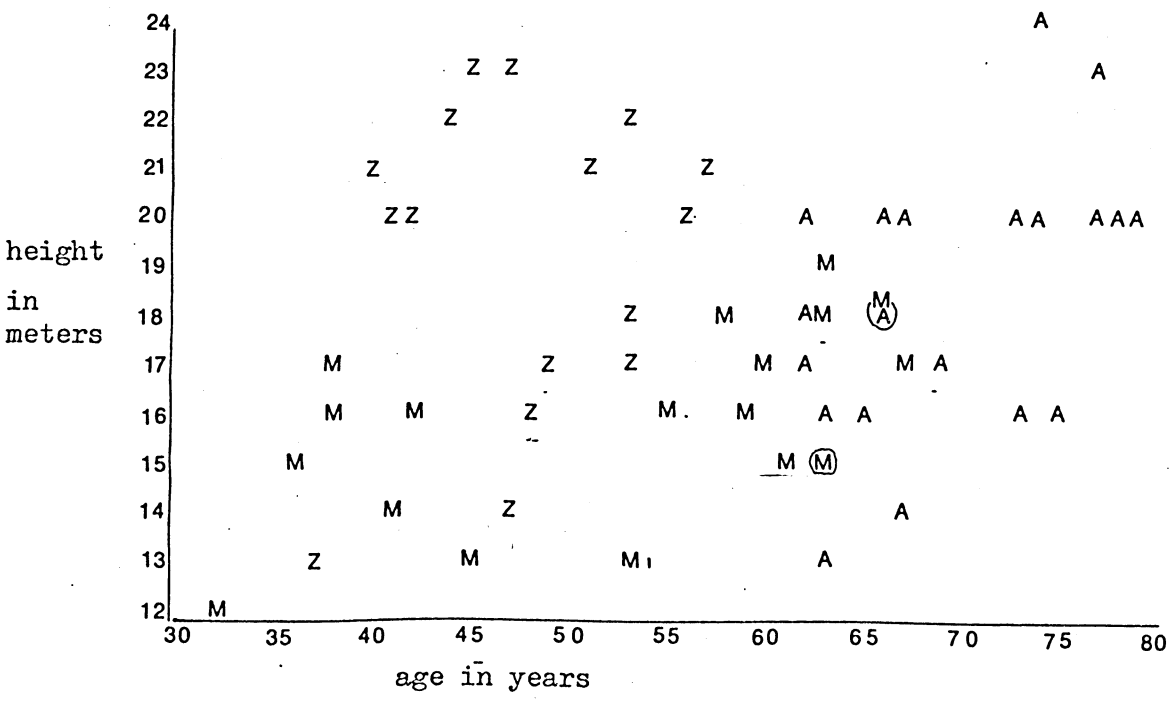
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age in years

Cedar Creek Natural History Area

Cedar Creek Natural History Area is located on the Anoka Sand Plain in east-central Minnesota. Cooper (1935) described the sand plain as an outwash plain of the Grantsburg Sublobe of the late Wisconsinan glaciation. The sands were deposited as river sediment when the Mississippi River flowed over the receding ice. The normal southeast drainage of the Mississippi had been blocked by the Grantsburg Sublobe, but as it receded the land's slope to the south remained, and the river gradually shifted west across the thinning ice leaving a flat sand area.

Stand description and discussion:

The study area in Cedar Creek was in SW 1/4 NW 1/4 sec. 27, T. 34 N., R. 23 W., Anoka County. Pierce (1954) reviewed the history of the natural area. The federal land survey was made in 1849 and 1854. It described the area as oak openings on sandy soil. Red oak was not listed among the witness trees; black oak (northern pin oak) was a common tree. Pierce found that oak forests were the dominant vegetation type, and the oaks were the northern pin oak and bur oak, both indicators of the xeric conditions caused by the rapid drainage of the soils. The precipitation is 67.5 cm/year at Cambridge, the nearest meteorological station. That is

7 cm/year greater than in Itasca Park. The soils are classed as fourth-rate podzols by the local Soil Conservation Service (Pierce, 1954). On the knoll in the present study area, Pierce found a red oak-sugar maple-basswood forest, with northern pin oak as a subdominant. The study areas are Crone's Knoll, a deciduous island in a cedar bog (surrounded by oak forest and old fields), and the edge of a field located between the sand soil and the cedar bog.

Crone's Knoll has been somewhat disturbed by man in the past. There is a cabin and occasional planted trees. There is a continuous canopy of the deciduous dominants and a few Pinus strobus. Seedlings of the dominants, Carex spp., and herbaceous growth of spring ephemerals form a continuous surface cover. There is some shrub growth in patches, but without the species indicative of extreme disturbance; no Zanthoxylum americanum, Ribes spp., or Rubus spp. are in the area studied.

The woods at the edge of the old field seems younger than the woods on Crone's Knoll: most of the trees are smaller and there are many of sapling size. The herb layer forms an interrupted surface cover. Many ferns occur in the shrub layer. There is a full shrub layer, mostly of Alnus rugosa, and sapling-sized Populus tremuloides, Amerlanchier spp., and several Quercus species. The canopy is interrupted to continuous,

but lower than the Crone's Knoll canopy. There are no basswood among the trees within 10 meters of the specimen trees, although there are several red maples of quite large size. There are white and bur oak growing among the northern pin oak-type trees. These are both of the white oak subgenus, which is not known to hybridize with the black oaks.

The conditions at the edge of the old field may be more droughty than on Crone's Knoll because of greater exposure and proximity to the sand soil of the field. (The Alnus shrubs were at the bog side of the narrow forested strip next to the meadow. They are within ten meters of the oak trees, but are lower than most of the oaks.) The climatic factors ought to be the same for both stands, but the edaphic conditions are different. Cedar Creek, then, does not provide a control to test the question of genetic or environmental control of oak differentiation.

Taxonomy of Quercus borealis and Q. ellipsoidalis

The two oaks of interest in the present study are Quercus borealis Michx. f. (= Q. rubra L., which Trelease suggested was ambiguous) and Q. ellipsoidalis E.J. Hill. These species are part of the red oak complex (a section of the Erythrobalanus) comprised of Q. borealis, Q. coccinea, Q. ellipsoidalis, Q. falcata, Q. schumardii, and Q. texana (Richens, 1945). This is essentially the Coccineae of Palmer (1942) and the Coccineae plus the Pagodaefoliae of Trelease (1924). Palmer (1942) considered them all interfertile.

In its wide range (most of the US east of the Dakotas) red oak contacts many localized species, and hybrid individuals often result. In Minnesota, the range extends westwards to Polk and Becker Counties (fig. 5).

The habitat of the red oak is the most mesic of the black oaks. In Wisconsin, it does best on deep, well drained soils with good moisture and nutrient supplies. The trunks are susceptible to fire damage and there is generally poor regeneration (Curtis, 1959), although Auclair and Cottam (1971) found that red oak is capable of sprouting back after severe logging. Kell (1938) considered red oak to be a permanent species

of the maple-basswood forest in northern Minnesota where it ranks fifth in density after Acer saccharum, Tilia americana, Ostrya virginiana, and Ulmus americana.

Little (1971) showed that Q. ellipsoidalis is distributed in Minnesota and Wisconsin, and the northern parts of Indiana, Illinois, and Iowa. It has the most xeric habitat of the red oaks. Northern pin oak is found in pure stands in Wisconsin only on dry sandy soils. It is susceptible to fire, but root-sprouts readily when the trunk has been damaged (Curtis, 1959).

Red oak and northern pin oak are separated in taxonomic manuals by morphological characters. Table 3 lists characters used in the present study to differentiate between the species from field descriptions. For all characters a feature like red oak was given a value of one, intermediacy was rated at two, and a state like northern pin oak was given a value of three. Values were then doubled for quantitative characters, to give them greater weight than the more subjective qualitative data.

Not all of the characters are considered equally valid in distinguishing the species. Dyal (1936) separated northern pin oak from similar species only on the basis of habitat, bud characters, and distribution. Trelease (1924) did not consider that leaf persistence is a good taxonomic character, at least for the south where deciduous and evergreen species overlap.

Figure 5. Minnesota Distribution of Quercus borealis and Quercus ellipsoidalis.

● - Quercus borealis (including specimens labeled Q. borealis var. maxima.)

□ - Q. ellipsoidalis

From University of Minnesota Botany Herbarium distribution maps.

Morley (personal communication) considers leaf persistence to be a function of age of the tree. I used this character only for the Cedar Creek trees that were observed in the spring. Trelease found flower parts of all oaks to be similar. I attempted to measure flowers from the Cedar Creek trees and classify them according to descriptions from manuals. This was not possible because catkins keep growing. Unless trees are observed and records kept from the first appearance of the flowers, there is no way to correlate measurements or descriptions such as crowded or sparse. Morley (1972) considers the acorn-cup ratios (inner width to inner depth) to be the best way to differentiate between species. Leaf form is widely used and widely distrusted. Upper crown leaves would be most reliable, but in the present study they were impossible to obtain.

The traits from the trees are not weighted except for the quantitative ones. This not because they are equally good traits, but because they all contain inaccuracies. Tree shape depends on age and environmental conditions (openness of growing area and wind damage are only two obvious influences). Branch shape is somewhat better, but is generally interpreted in relation to what one is seeing that day, not in relation to a theoretical standard. Branch persistance is affected by proximity of other trees, but does vary among trees

in apparently equivalent habitats. It is determined in relation to other trees in the stand under consideration also. It is a fairly good trait when the observer has experience with forms of the pure species. Bark traits vary with the age of the tree and part of the tree viewed. Morley (personal communication) considers some of the northern pin oaks to have a distinctive rough pattern (the area between the many fissures is not flat), which grades into the flat ridges similar to those of the red oak. There appears to be broad overlap in bark texture, but old, seemingly pure individuals do have distinctive bark. Traits of old trees (more than 100 hears) are much easier to classify than are those of younger trees, in general.

Acorn and acorn-cup shape and color have broad ranges in the described forms of red oak. The longitudinal black stripes on the acorns and the smaller size of the nut and cup of the northern pin oak are good characters where red oak is the only other black oak around. These acorn traits do not hold true when Q. velutina occurs as well. Acorn data have the disadvantage of usually having to be gathered from acorns unattached to the tree. There are bound to be acorns attributed to the wrong trees. Large collections would lessen the impact of stray acorns, but that is seldom possible in a forest with an active squirrel population.

The color of acorns is a problem that would be possible to better define were color charts to be used, a possibility that applies equally to other parts of the trees that are described and segregated by color. The size of the acorns could be related to the climate: larger acorns might be produced in a moister habitat. Whether such a trait were genetically controlled, or directly affected by the habitat would have to be established experimentally.

Leaf characters would be very good if consistency of leaf location and degree of exposure to the sun could be obtained. Full sun leaves from the top of the crown would be the best leaves to use since the degree of shading (none for canopy trees) would be known and could be eliminated from consideration in analyzing numbers of lobes and indentation of sinuses. Degree of sublobing would be an interesting character to investigate: the northern pin oak appears, on casual review, to have far larger sublobes than the red oak. Only sun leaves could be used for such an investigation as sublobing seems to be minimal in shade leaves. All the leaf traits are affected by shading. Since all the leaves studied were exposed to different, unknown, amounts of shading, the leaf data ought not be viewed as providing absolute confirmation of differences, but rather as indicating that differences may exist. The data do sort into separate populations for each stand and herbarium

group. The greater leaf surface area of the red oak might be a result of the moist conditions of its preferred habitat. Again, large size could be genetic or it could be directly induced by the habitat.

The differences in color of the young leaves holds quite well, and although it can be used only in the spring, top leaves can be observed without removal from the tree, so it is a practical trait. It could be used for seedling studies of hybridization between red oak and northern pin oak. Pubescence is less visible with binoculars, and would be subjective in any case.

The value of considering reproduction in the shade is limited by the difficulty in ascertaining how long a seedling has survived. Seedlings of any reproducing species are bound to occur, the question is how long they survive. Sapling presence could be better used as in indication of reproduction. Experiments comparing relative survival in the shade would have to be run to determine whether the two species actually differ in their shade tolerance.

Leaf persistence may indeed be a function of age of the tree or state of health of the branch. Some trees do retain their leaves to spring, and these are seldom the tall, straight trees.

There appears to be some correspondence (fig. 6) between the ratio from the inner width to inner depth

of the acorn cups and the percent indentation of leaves from the same tree. There is a lesser trend toward fewer lobes with greater indentation. When such a plot is made of herbarium specimens there is segregation according to species, with some central overlap.

The results for the Itasca transect study area are of interest: each stand is quite consistent within itself. There is less indentation and greater lobing in leaves from the field samples than in the herbarium specimens. It is possible that the use of shade leaves from the study trees is a cause of the difference since shade leaves tend to be larger than sun leaves. If that is so, perhaps the fact that the trees in Z were subcanopy, producing greater shade for those leaves, explains why the leaves from Z have the least indentation. To conclude that the herbarium specimens are sun leaves is not possible since their location on the trees was not noted on the specimens. As the three quantitative traits appear, to some measure, to be correlated, and to coincide with species classifications, their value as indicators of species type is enhanced. Each trait is presented in frequency histograms in Appendix B.

Table 3. Taxonomic characters

	Trait:	Quercus borealis	Intermediate	Q. ellipsoidalis
1.	Tree shape	tall, straight	straight, but low fork	low forking branches
2.	Branch shape	straight		gnarled
3.	persistence	few	several	many low on trunk
4.	Bark color	gray	brown	dark brown, black
5.	fissures	deep		shallow
6.	texture	flat-topped ridges	mixed ridges and plates	flat plates or rough
7.	Acorn color	pale brown	dark brown, no stripes	dark brown, black stripe
8.	shape	ovoid or cylindrical	large, ellipsoid	ellipsoidal
9.	Acorn cup color	dark brown		pale brown
10.	shape	shallow, saucer shaped	large, tapering	tapering, turbinate
11.	size	covers 1/3 of nut		covers ½ to 1/3 of nut
12.	width:depth	2.1 - 4.8	2.0 - 2.2	1.1 - 2.1
13.	Leaf texture	thin	medium	thick
14.	color	dull, dark green above	green	shiny, bright green
15.	base	acute	rounded	truncate
16.	no. lobes	6.6-13.0 range average 9.1/leaf	7.7 - 9.1	range, 5.6-9.5 average 7.7/leaf
17.	sinus indent	range 40.5-82.4% average 63.3%	66.5 - 81.5%	average 81.5% range 66.5 - 94.4%
18.	Reproduction in shade	shade tolerant (seedlings present in sample area)		shade intolerant (no seedlings present)
19.	Color of young leaf	bronze until mature		early trace of red, very pale
20.	pubescence	soon glabrous		tardily glabrous
	Leaf persistence	drop in fall		persist to spring

Characters used for hybrid indices:

Itasca transect: 1-7, 9, 12-18.
Cedar Creek: 1-11, 16, 17, 19, 20.

From: Dyal, 1938; Fernald, 1950; Gleason and Cronquist, 1963; Hill, 1899; Morley, 1972; Rosendahl, 1955; Sargent, 1965; U of M herbarium.

Figure 6. Pictograph to relate leaf sinus indentation, number of lobes per leaf, and ratios of acorn cups.

A = tree from stand A

Z = tree from stand Z

M = tree from stand M

e = herbarium specimen labeled Quercus ellipsoidalis

b = herbarium specimen labeled Q. borealis

The number of lobes (average per tree) is portrayed as follows:

o 7 - 7.9

ó 8 - 8.9

ó 9 - 9.9

ó 10 - 10.9

ó 11 - 11.9

ó 12 - 12.9

Herbarium measurements are in Appendix D

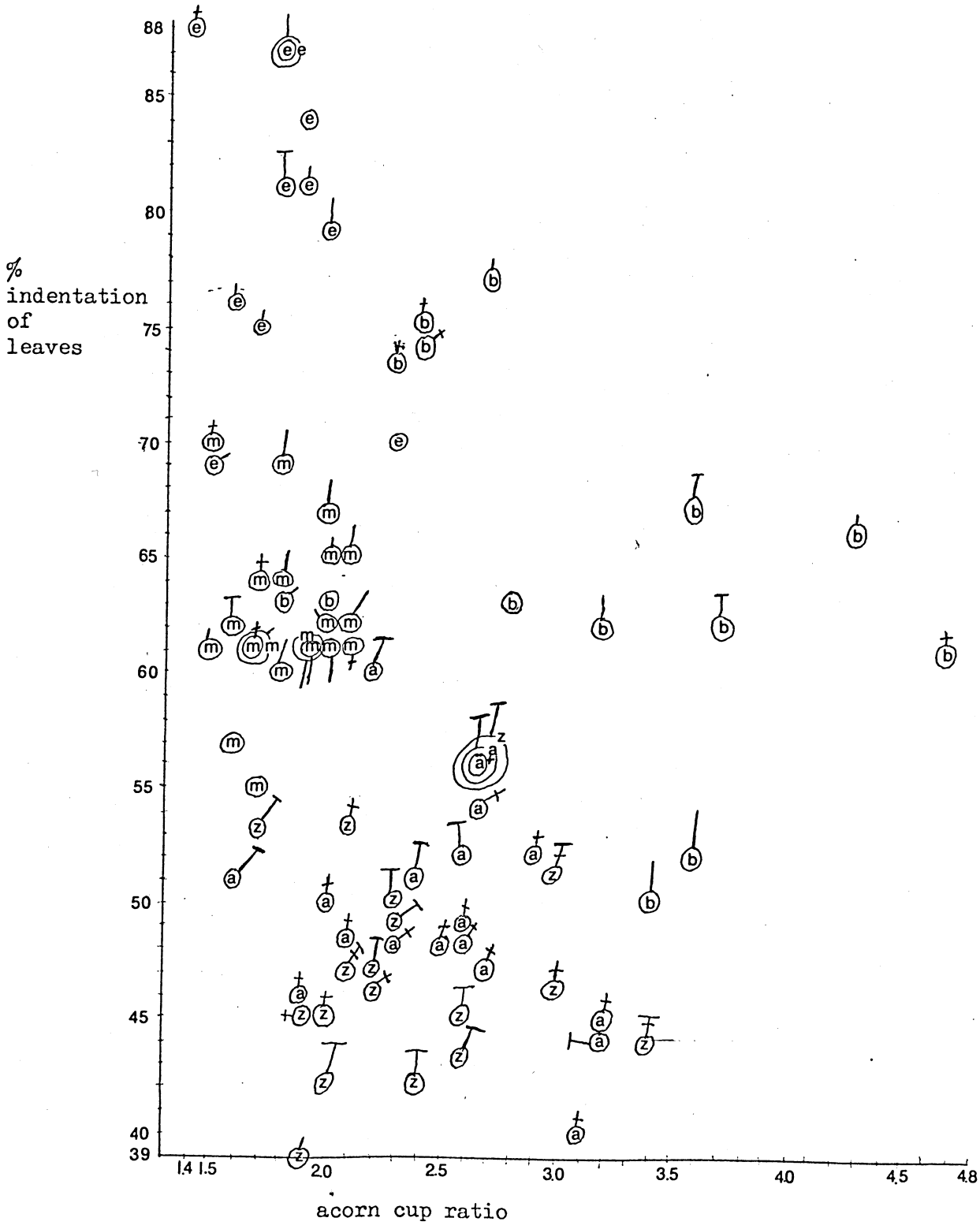

% indentation of leaves
88
85
80
75
70
65
60
55
50
45
40
39
1.4 1.5
2.0
2.5
3.0
3.5
4.0
4.5
4.8
acorn cup ratio

Figure 7. Representative leaf and acorn types

a) Q. borealis-type leaf - this one is from stand A

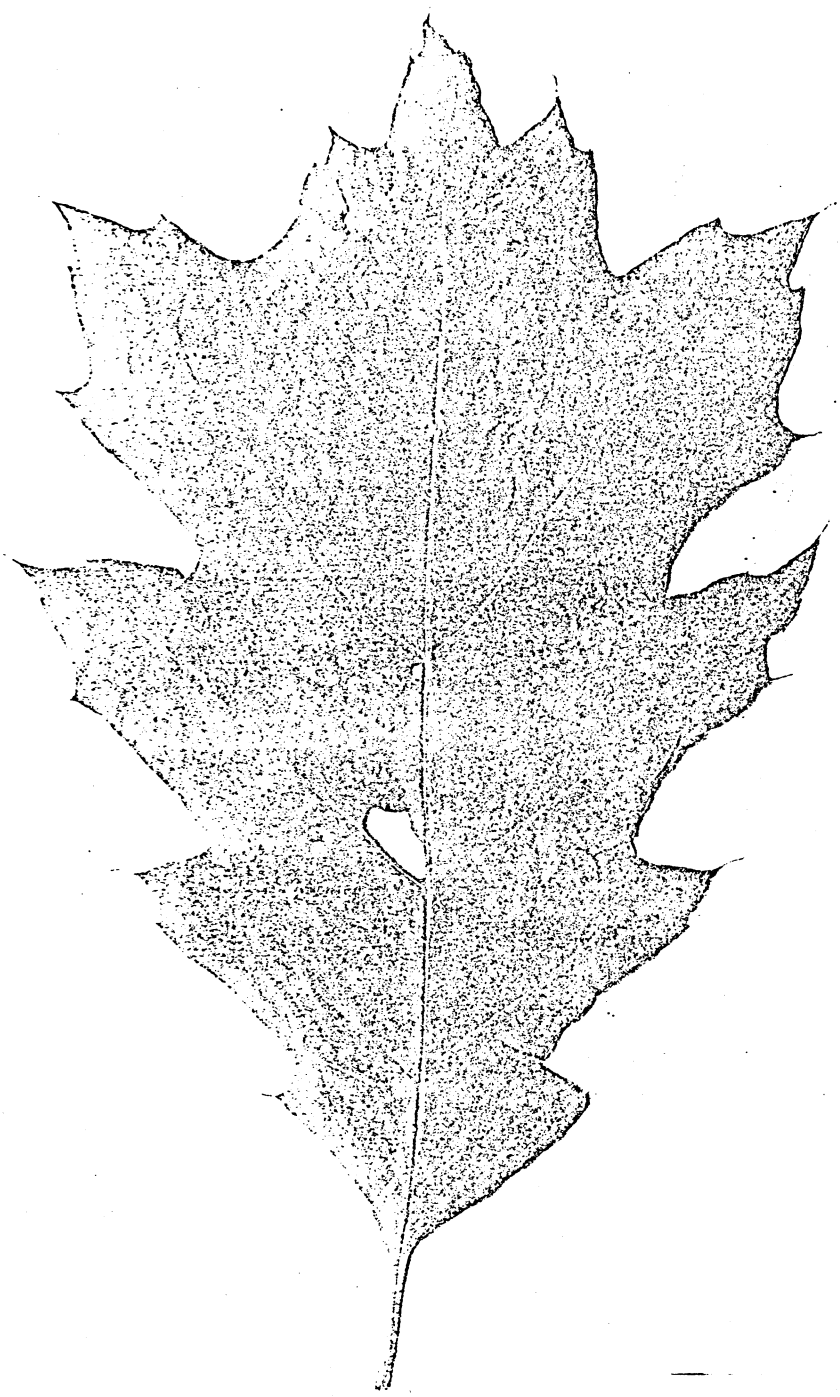
b) Q. ellipsoidalis-type leaf - this one is from stand M

c) acorns and cups

   i. Q. borealis-type

   ii. Q. ellipsoidalis-type

a.



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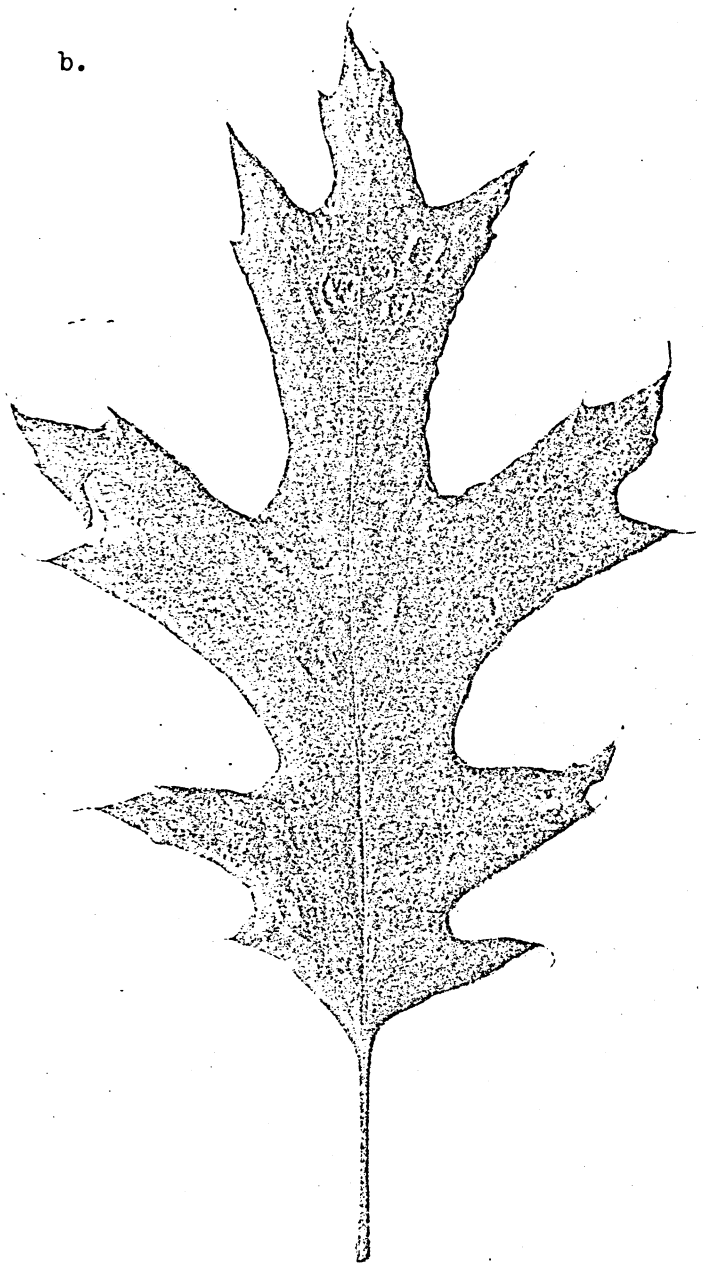
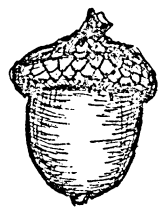


c.

i.



ii.

Controls on *Quercus* hybridization

Incompatibility of one species to the pollen of other species is often cited as a method of maintaining species integrity. Among the oaks the only demonstrated incompatibility has been between the species of the different subgenera. Pjatnitsky (1946) attempted many crosses between taxonomically differentiated species. He found that only when he crossed species of different subgenera were there no hybrids produced. *Quercus borealis* was the only representative of *Erythrobalanus*. When it was the female parent, no offspring were produced. With *Q. borealis* as the male parent there were essentially no viable acorns produced when the female was of a species of *Lepidobalanus*. There were a few surviving young when the cross was with a member of *Mesobalanus*, which does not occur in North America.

Many authors have felt that there are other isolating mechanisms at work to maintain separate species. Stebbins, et al. (1949) stated that seasonal isolation was of little importance in the oaks. In the present study, the trees at Cedar Creek were found to have very similar flowering times in the spring of 1971. A survey of the dates on flowering specimens from Minnesota in the University of Minnesota herbarium for *Q. borealis* and *Q. ellipsoidalis* supports the observation. Dates for red oak were from May 8 to June 3, in twelve

different years (13 specimens). Northern pin oak dates were from April 19 to June 6 in seven years (15 specimens).

Stebbins et al. (1947) suggested that there might be slight imcompatibility to foreign pollen and reduced viability of hybrid embryos. Because of the many acorns produced and the few that grow, even a small discrimination against hybrids would reduce production of hybrid adults in a mature forest. This hypothesis has not been tested experimentally.

Muller (1952) cited ecological factors as controls against natural hybridization in Quercus. Species need to share pollen in order to produce hybrids: overlapping ranges would best provide the needed proximity. Intermediate habitats for the F_1 hybrids would be necessary. Climatic and edaphic factors would have to be conducive to hybrid growth.

Anderson (1948) felt that sterility was not the solution to the relative lack of hybrids in nature, a theory that has been demonstrated for the oaks at least. Backcrosses would remove the obviousness of hybrids, except where hybrid habitats exist. Wiegand (1935) concluded that species were more uniform away from the disturbed areas in which hybrids would occur.

Some species hybridize with each other in parts of their range and not in others. Muller (1952) cited several examples from Texas and hypothesized that in some of the smaller, hybridizing groups the genes that

prevent crossing elsewhere might have been lost. Red oak and northern pin oak are thought to hybridize in northern Minnesota, but appear to do so less commonly in the southern part of the state where other black oaks occur (E.J. Cushing, personal communication).

This inconsistency of incompatibility supports Stebbin's (1950) view that gene mutation has been the method of evolution among oaks. If only a few genes are involved as isolating mechanisms, these could be easily lost through genetic drift or deletion from a small population. Stebbins based his hypothesis on the fact that all Quercus species have similar chromosomes. All oaks have $n = 12$ chromosomes (Sax, 1930; Duffield, 1940; and Richens, 1945). There is also a uniformity of pollen grain size and viability, which I tested from eight trees at Cedar Creek. Sax (1930) reported 3-10% sterility from both pure forms and hybrids. Six of the trees at Cedar Creek, all close to but not matching northern pin oak (by morphological characters) had pollen sterility within the 3-10% limits. Two other trees had about one-third of the tested grains (more than 275 total counted for each tree) inviable. One of these trees had very few catkins which, in turn, contained less pollen than the other trees. There were no acorns below that tree. These two trees were similar in morphological characters to the other six. Pjatnitsky

(1946) and Ness (1927) have reported individual trees that were sterile or poor seed producers: these two trees may be such aberrant individuals. The causes of such sterility have not been explained.

Conclusions

Scatter diagrams were made on the basis of fifteen qualitative and quantitative characters. In fig. 7, intermediate characters are included in the totals for each species, which results in a skewing of the scatter away from the diagonal. (Fig. 9 shows the intermediate traits weighted correctly.) In fig. 8, traits with intermediate expression were deleted from the totals; it is included to demonstrate the lack of pure Q. ellipsoidalis in the stands sampled in the Itasca transect. This could to some extent, be due to classifying as red oak traits that are actually indefinite, such as bark texture. Because 15 traits are used influence of such overlap should be minimal. The major scatter may be attributable to backcrossing of hybrids with red oak, producing the inclination towards Q. borealis traits. It could also be due to the climate and soils being more mesic than xeric, which may select for red oak-type traits, whatever the genotype of the individual.

The most intermediate trees were from stand M. The environment there matches the xeric habitat of northern pin oak, but is on rich soil such as red oak is considered to require (Curtis, 1959). This is an intermediate habitat of the variety postulated for hybrids. Both species have been recorded north, south, and east

of stand M (fig. 5), but never in Mahnomen County (likely because of lack of collecting rather than non-existence there). Eastward the climate becomes less rigorous and more mesic; perhaps there is selection for red-oak traits.

Stand A has the most trees of the red-oak type. Stand A also is the oldest stand, which could indicate bias in the field descriptions of the trees, because of age affecting the conformation of the trees. Such bias may exist, but stand M was not the youngest stand, and its trees occur closest to the northern pin oak-type on the scatter diagrams.

There is differing expression of morphological characters from tree to tree at Cedar Creek as well as among the trees in the Itasca transect. The stands at Cedar Creek are within a few hundred meters of each other. There, then, differences in climate would not be as great as from stand A to stand M. There are differences among the trees on Crone's Knoll, which are not only close together but are all in the forest, are all large trees, and all are on similar soil. That group of eight trees ranges from very similar to red oak to intermediate between the two species (fig. 7). The remaining trees at Cedar Creek are close to northern pin oak, but are not perfect examples of that type. If hybridization is causing the variation in form these trees would seem to be backcrosses to northern pin oak.

Figure 8. Scatter diagram based on 15 characteristics, intermediately expressed traits are counted in the totals of both species

a. Itasca transect

b. Cedar Creek

A = one tree from stand A

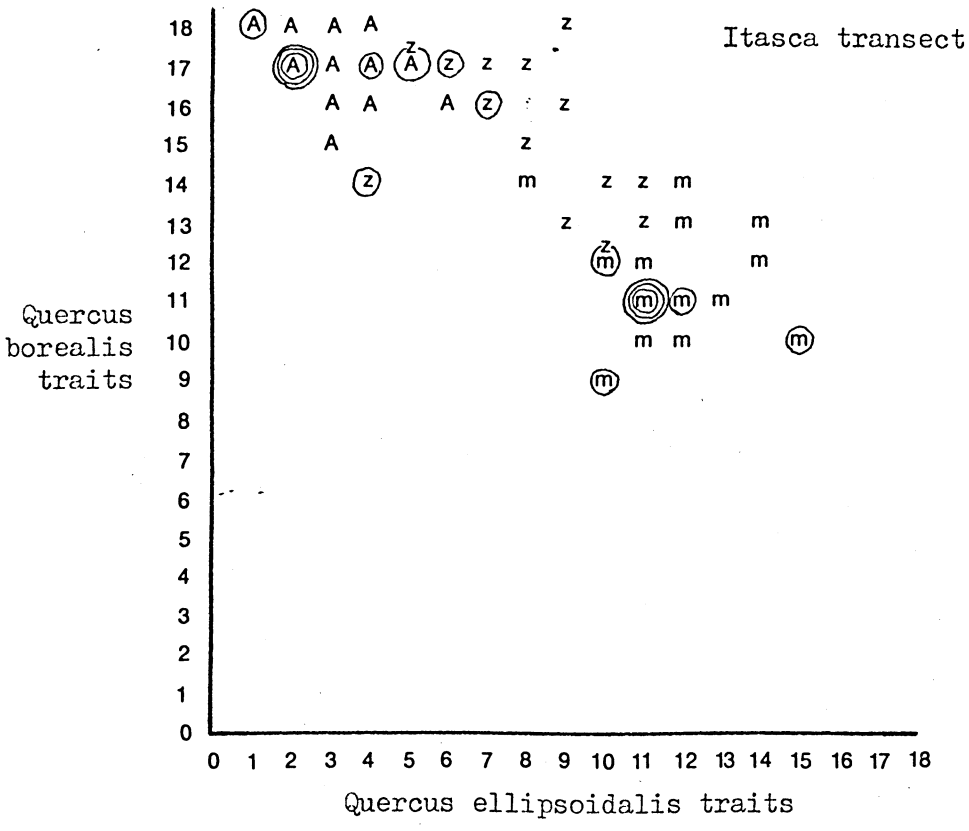
z = one tree from stand Z

m = one tree from stand M

c = one tree from Crone's Knoll

s = one tree from the edge of the field

A circle around a letter, Ⓐ, signifies one additional tree with the same total traits of each type.


Itasca transect
Quercus borealis traits
Quercus ellipsoidalis traits

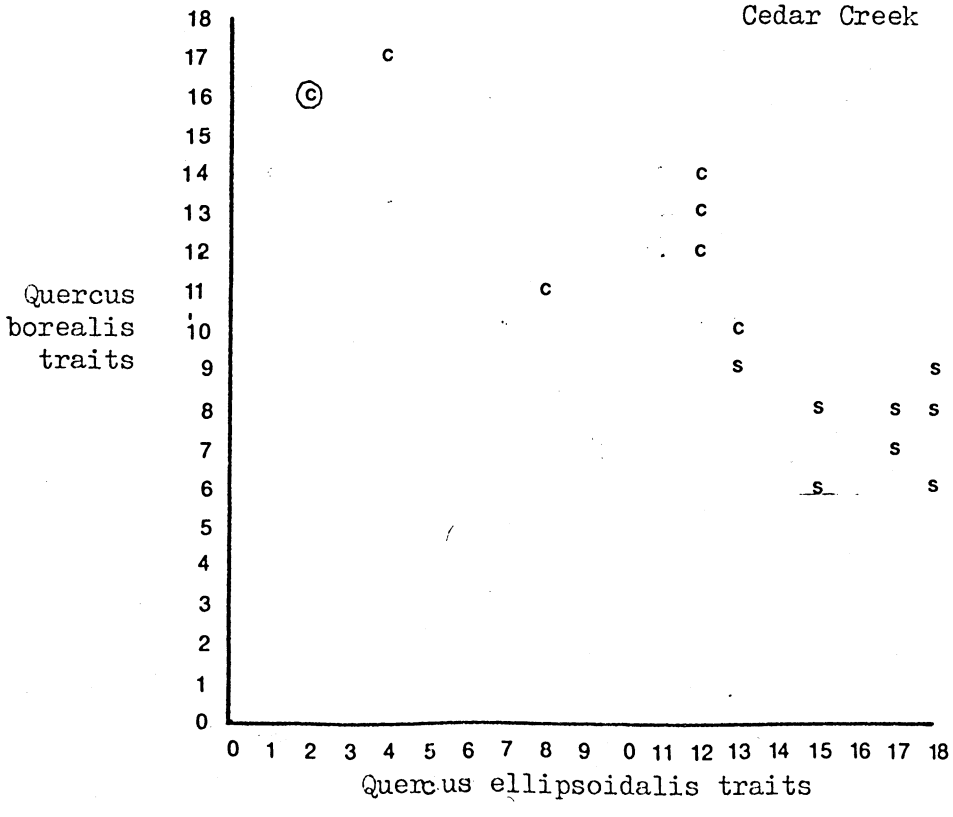

Cedar Creek
Quercus borealis traits
Quercus ellipsoidalis traits

Figure 9. Scatter diagram, intermediately expressed traits not included

a. Itasca transect

A = one tree from stand A

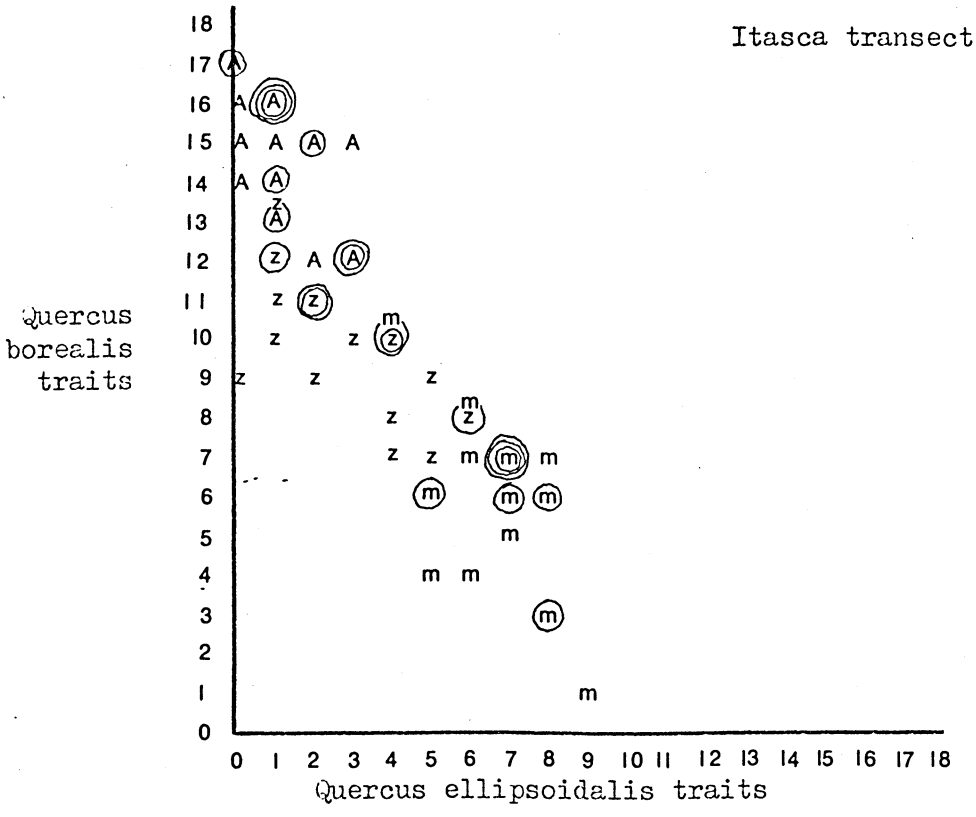
z = one tree from stand Z

m = one tree from stand M

b. Cedar Creek

c = one tree from Crone's Knoll

s = one tree from the stand at the edge of the field


Itasca transect
Quercus borealis traits
Quercus ellipsoidalis traits

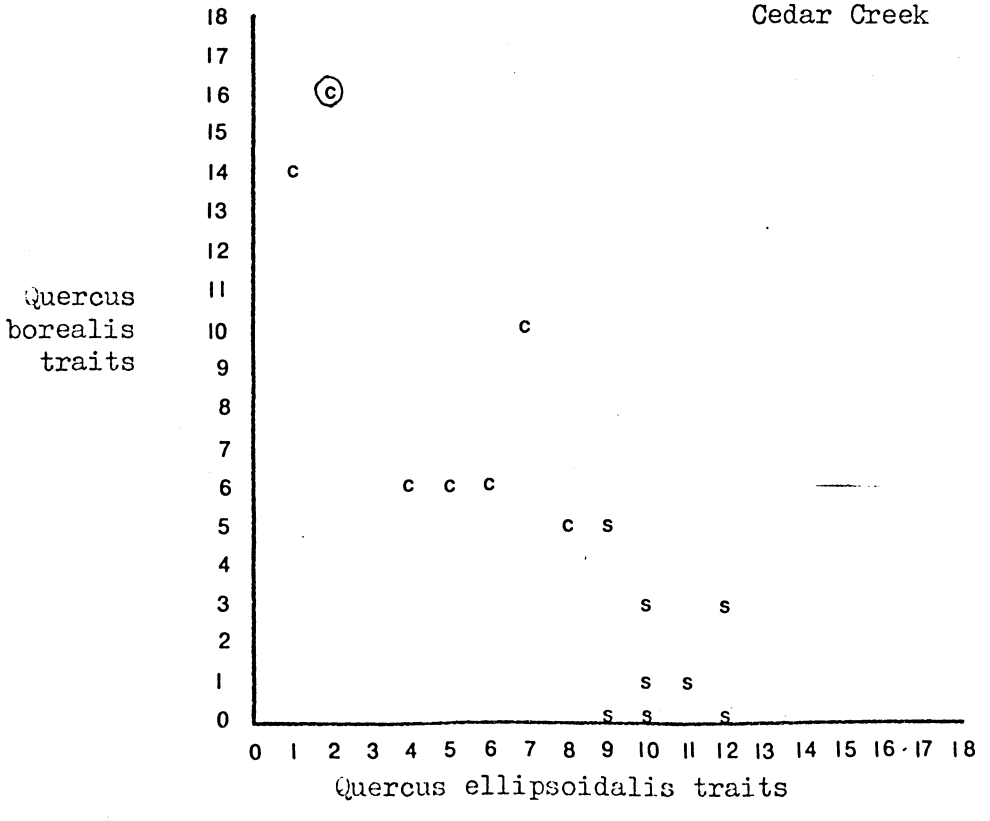

Cedar Creek
Quercus borealis traits
Quercus ellipsoidalis traits

Figure 10. Histograms showing positions of trees relative to reference phenotype

Quercus borealis = 18 from reference characters

Q. ellipsoidalis = 54 from reference characters

A = trees from stand A

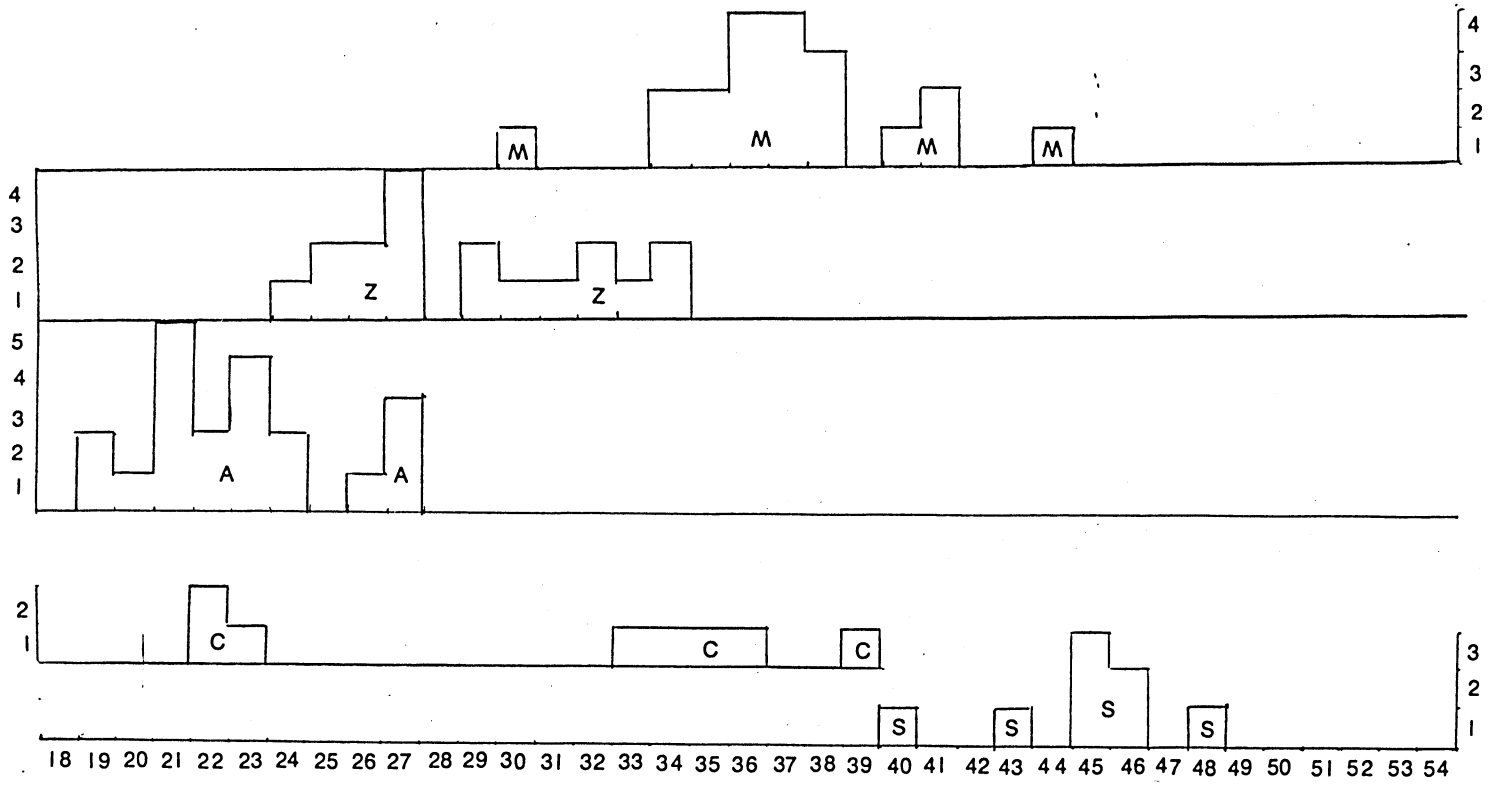
M = trees from stand M

Z = trees from stand Z

c = trees from Crone's Knoll

s = trees from stand at the edge of the field

Based on 15 characters



18 = Quercus borealis, from 15 reference characters

54 = Q. ellipsoidalis, from 15 reference characters

If the variation is environmentally produced, it would be difficult to decide what environmental factors are causing the variability.

Since no breeding experiments were carried out, the trees in this study cannot be absolutely identified as hybrid. There are specimens in the Botany herbarium dating from 1933 that are labeled Q. borealis x ellipsoidalis, so the possibility of hybridization has been considered for many years. Morphological variation among the stands does exist at both Cedar Creek and in the Itasca transect. It is conceivable that since the changes follow habitat variation, the changes are environmentally induced. Given the demonstrated proclivity of oaks to hybridize, I feel that there is a good chance that there is hybridization between the northern pin oak and red oak, which may be emphasized by the habitat differences of the stands studied.

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Appendix A

Stand A

SE 1/4, NW 1/4, SW 1/4 SEC 24, T. 143 N., R. 36 W.

Point-quarter trees:

Density = 600 trees/ha
Dominance = 29 m^2/ha
mean B.A. = .048 m^2 per tree

Oak trees:

mean age = 70 years
age range: 62-79 years
mean height = 18 m
height range: 13-24 m

Point-quarter trees:

	Density (trees/ha)	% Freq.	Dom. (m^2/ha)	I.V.	10^2 seedlings/ha
Acer rubrum	53.5	30	1.85	9.1	180
A. saccharum	38.1	20	1.04	5.9	190
Amelanchier sp.					15
Betula papyrifera	91.6	45	3.72	15.3	2.9
Ostrya virginiana	1.7	5	.07	1.2	38
Pinus strobus					.32
Populus grandidentata	129.5	45	8.21	22.6	3.5
P. tremuloides	53.5	20	4.85	10.1	8.0
Prunus serotina					1.9
P. virginiana					21
Quercus borealis-type	200.0	75	9.07	31.5	31
Q. macrocarpa	15.5	10	.21	2.3	
Tilia americana	1.7	5	.68	1.9	1.6

Area sampled for seedlings, saplings, and shrubs = 312.8 m^2.

Density of saplings = 4 x 10^2/ha

Density of seedlings = 5 x 10^4/ha

Stand Z. NE 1/4, NE 1/4, NE 1/4 sec. 5, T. 142 N., R. 36 W.

Point-quarter trees:

Density = 700 trees/ha
Dominance = 33 m^2/ha
mean B.A. = .044 m^2

Oak trees:

mean age = 48 years
age range: 37 - 57 years
mean height = 18 m
height range: 13 - 23 m

Point-quarter trees:

	Density (trees/ha)	% Freq.	Dom. (m^2/ha)	I.V.	10^2 seedlings/ha
Acer rubrum	18.5	45	0.24	7.9	43
A. saccharum					.68
Amelanchier sp.					22
Betula papyrifera	83.1	100	3.06	33.1	1.4
Ostrya virginiana					3.8
Pinus resinosa					13
Populus grandidentata	46.2	35	2.14	9.6	.34
P. tremuloides	489.3	25	22.67	39.1	1.3
Prunus serotina					27
P. virginiana					27
Quercus borealis-type	83.1	10	3.68	91	8.5
Q. macrocarpa	18.5	5	0.72	2.3	2.0

Area sampled for seedlings, saplings, and shrubs = 293.0 m^2.

Density of saplings = 5 x 10^2/ha

Density of seedlings = 1.5 x 10^4/ha

Stand M NW 1/4, NE 1/4, NW 1/4 sec. 5, T. 143 N., R. 40 W.

Point-quarter trees:

Density = 650 trees/ha
Dominance = 34 m^2/ha
mean B.A. = .053 m^2

Oak trees:

mean age = 52 years
age range: 32 - 67 years
mean height = 16 m
height range: 12 - 19 m

Point-quarter trees:

	Density (trees/ha)	% Freq.	Dom. (m^2/ha)	I.V.	10^2 seedlings/ha
Acer rubrum					.74
Amelanchier					15
Betula papyrifera					1.4
Fraxinus pennsylvanica					23
Populus deltoides					.74
P. tremuloides	105.6	40	4.38	15.3	5.9
Prunus serotina	16.3	10	.55	2.8	5.6
Quercus borealis-type	219.8	80	17.02	39.1	2.6
Q. macrocarpa	260.0	90	11.09	36.9	.74
Tilia americana					.32
Ulmus americana	48.8	15	1.36	5.8	1.1
Prunus virginiana					75

Area sampled for seedlings, saplings, and shrubs = 269.9 m^2.

Density of saplings = 6×10^2/ha

Density of seedlings = 1.3×10^4/ha

Saplings: number/ha

	Stand A	Stand Z	Stand M
Acer rubrum	96	273	
A. saccharum	96		
Betula papyrifera		34	
Ostrya virginiana	64	34	
Populus tremuloides	96		37
Prunus virginiana		34	
Quercus borealis-type		34	74
Q. macrocarpa		68	408
Tilia americana	64		
Ulmus americana			37

Shrub layer species and distribution

	A		Z		M	
	m^2	%T	m^2	%T	m^2	%T
Acer negundo					6.3	4.2
A. spicatum			.2	.1	4.0	2.7
*(Apocynum androaemifolium)	5.5	4.4	.4	.2	1.9	1.3
(Aralia nudicaulis)	13.6	10.9	12.4	6.2	14.9	10.0
Cornus alternifolia			10.5	5.2	3.5	2.4
C. rugosa	7.1	5.7	10.3	5.1	17.7	11.9
C. stolonifera			1.4	.7		
Corylus americana					24.2	16.3
C. cornuta	54.4	43.7	120.1	59.7	29.8	20.0
Craetagus sp.			4.0	2.0	1.4	.9
Diervilla lonicera	.8	.6	3.7	1.8		
Lonicera canadensis					1.1	.7
(Matteucia struthiopteris)			.7	.4		
Parthenocissus vitacea					11.1	7.5
(Pteridium aquilinum	27.0	21.7	10.9	5.5		
Rhus radicans	.1	.1	.3	.2	11.2	7.5
Ribes cynosbati					2.1	1.4
Rosa blanda	.2	.2	.7	.4		
Rubus sp.	1.7	1.4	1.7	.8		
Salix discolor					1.9	1.3

continued

continuation of previous page

	A		Z		M	
	m^2	%T	m^2	%T	m^2	%T
Symphoricarpos sp.					1.9	1.3
Vaccinium angustifolium	3.5	2.8	7.9	4.3		
Viburnum rafinisquianum	10.7	8.6	15.3	7.6	7.7	5.2
Zanthoxylun americanum			.1	.1	10.1	6.8
Totals	124.6	100.1	200.1	100.5	148.9	100.1
Total number of species	11		18		16	

*( ) non-shrubs included in shrub layer

Appendix B

Frequency distribution -- mean number of lobes in each sample

A = stand A

Z = stand Z

M = stand M

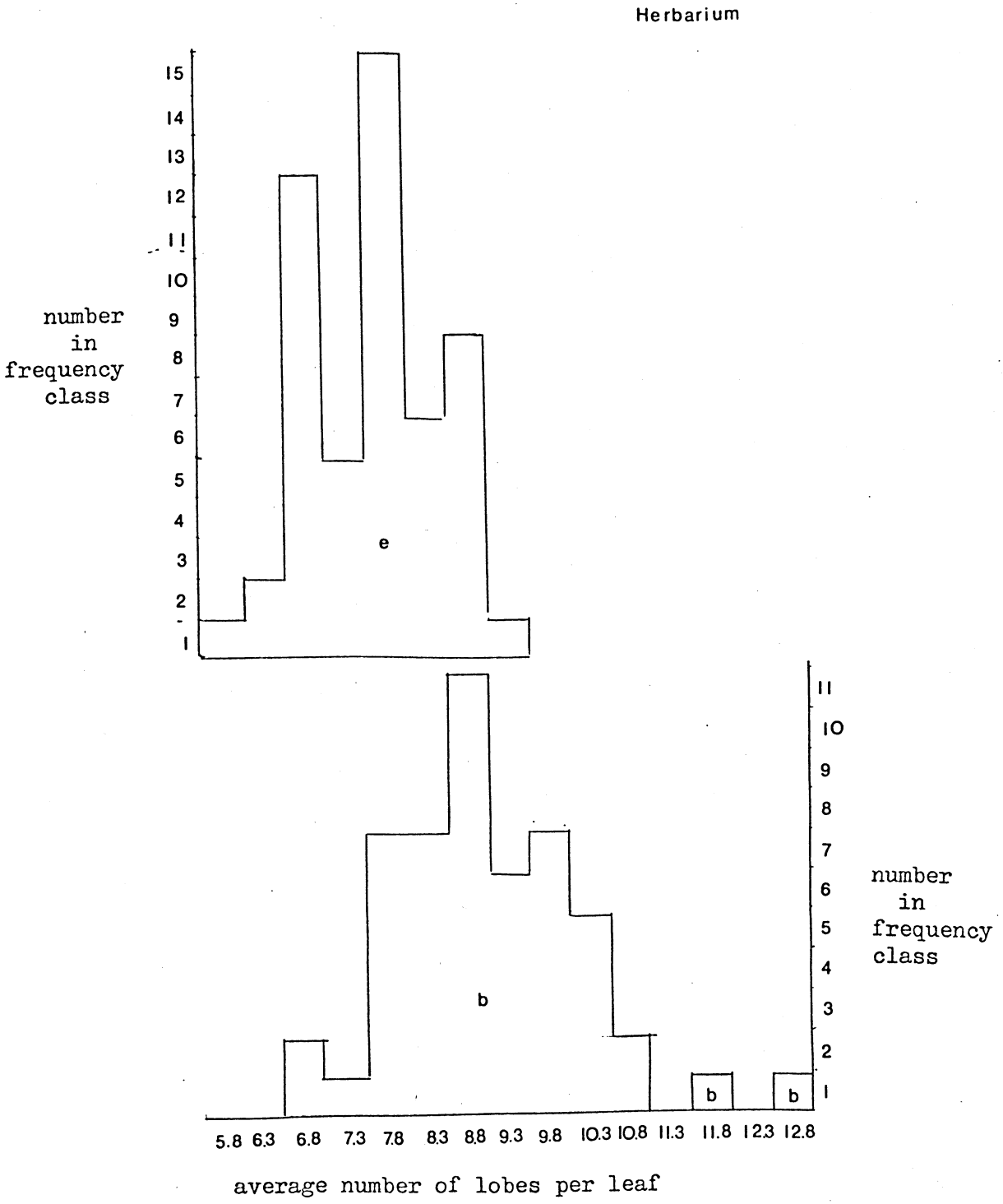
(next page)

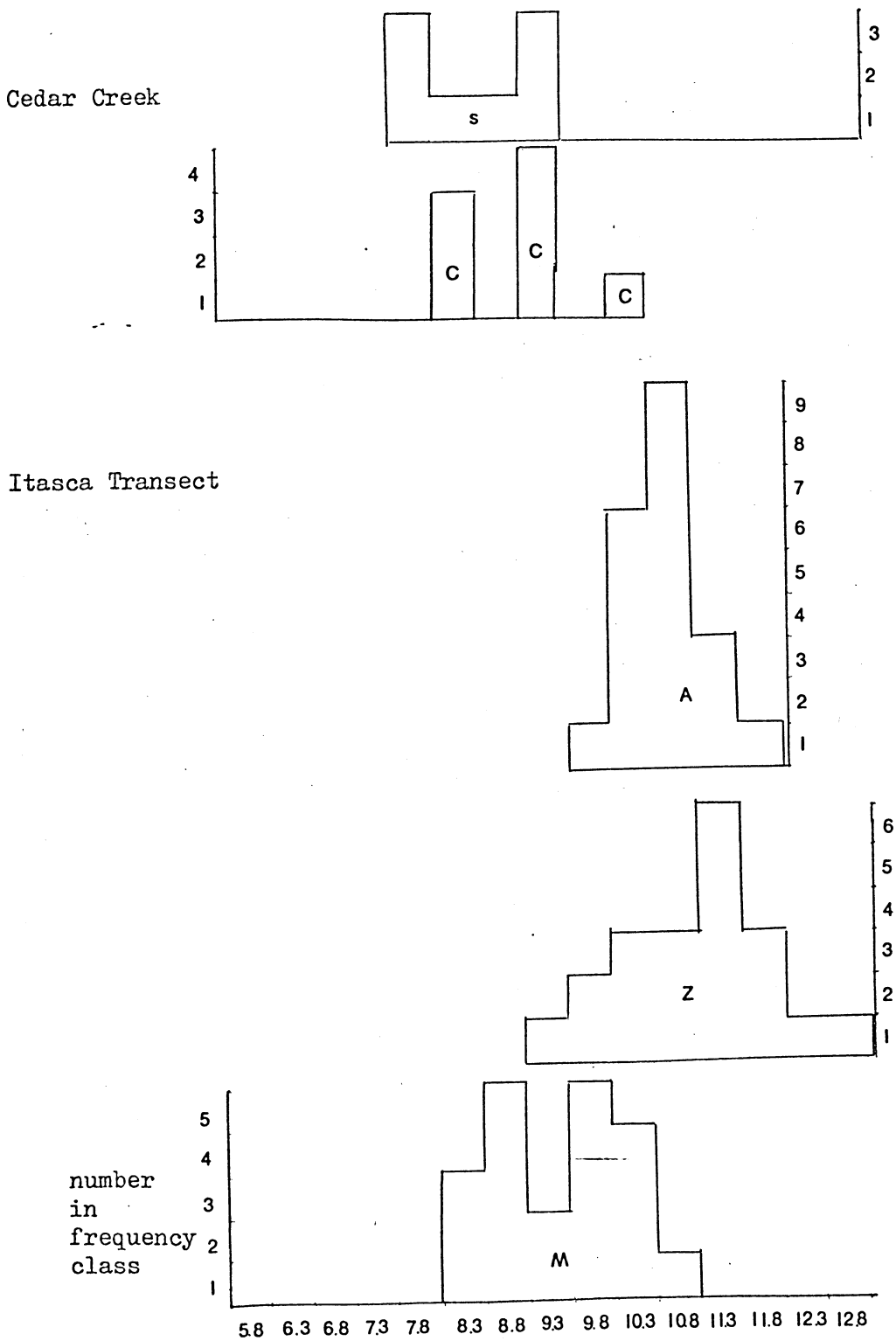
c = Crone's Knoll, Cedar Creek

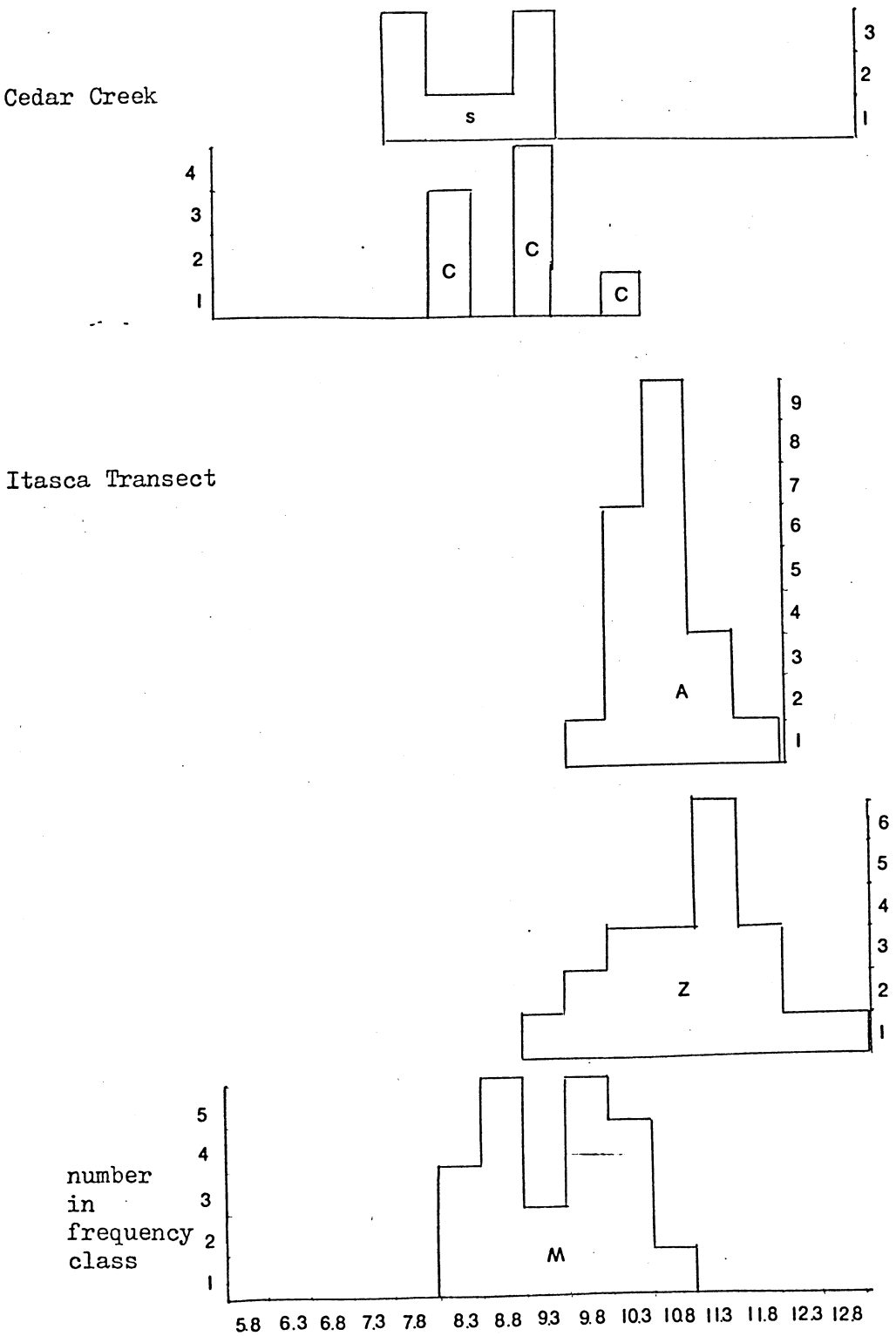
s = stand at the edge of the meadow, Cedar Creek

b = *Quercus borealis*, from herbarium

e = *Q. ellipsoidalis*, from herbarium


Herbarium
number in frequency class
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
e
b
b
b
11
10
9
8
7
6
5
4
3
2
1
number in frequency class
5.8 6.3 6.8 7.3 7.8 8.3 8.8 9.3 9.8 10.3 10.8 11.3 11.8 12.3 12.8
average number of lobes per leaf


Cedar Creek
S
C
C
C
Itasca Transect
A
Z
M
number in frequency class
5.8 6.3 6.8 7.3 7.8 8.3 8.8 9.3 9.8 10.3 10.8 11.3 11.8 12.3 12.8
average number of lobes per lobe


Cedar Creek
S
C
C
C
Itasca Transect
A
Z
M
number in frequency class
5.8 6.3 6.8 7.3 7.8 8.3 8.8 9.3 9.8 10.3 10.8 11.3 11.8 12.3 12.8
average number of lobes per lobe

Frequency distribution--mean % indentation of leaf sinuses

Itasca transect

A = stand A

M = stand M

Z = stand Z

Cedar Creek Natural History Area

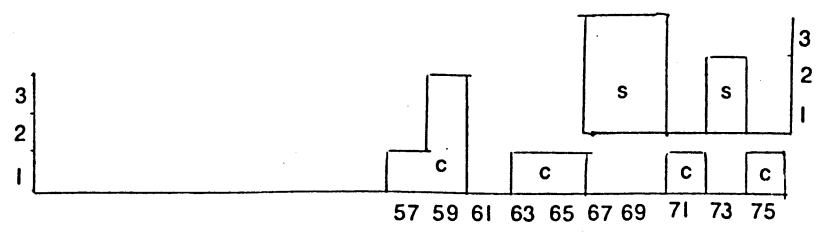
c = Crone's Knoll

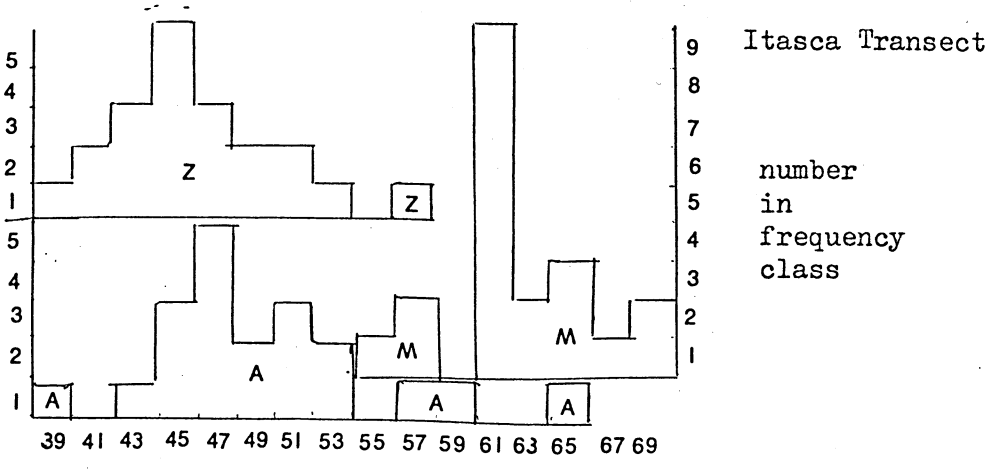
s = edge of the meadow

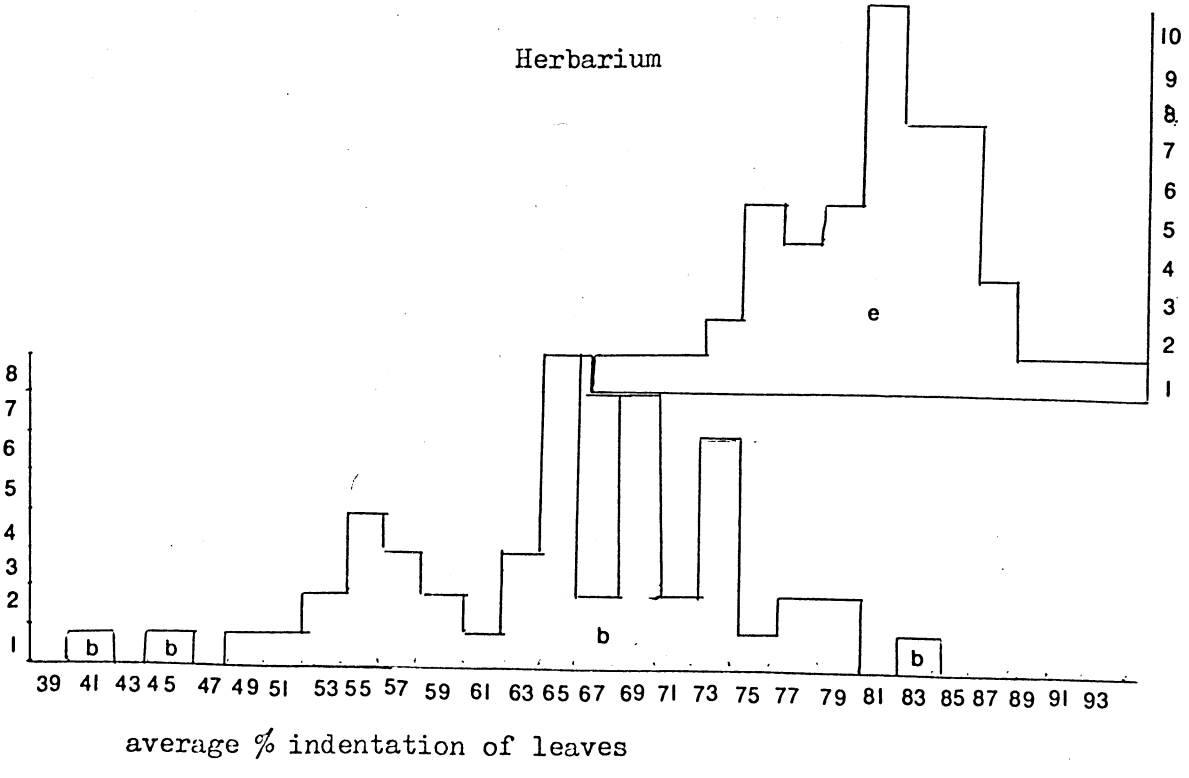
Herbarium

b = Quercus borealis

e = Q. ellipsoidalis


Cedar Creek
3
2
1
s
s
c
c
c
c
57 59 61 63 65 67 69 71 73 75


Itasca Transect
number in frequency class
Z
Z
A
M
M
A
A
A
39 41 43 45 47 49 51 53 55 57 59 61 63 65 67 69


Herbarium
e
b
b
b
39 41 43 45 47 49 51 53 55 57 59 61 63 65 67 69 71 73 75 77 79 81 83 85 87 89 91 93
average % indentation of leaves

Frequency distribution - acorn-cup ratios

Itasca transect

M = mean ratio of inner width to inner depth of acorn cups from one tree of stand M

A = stand A, distribution of means

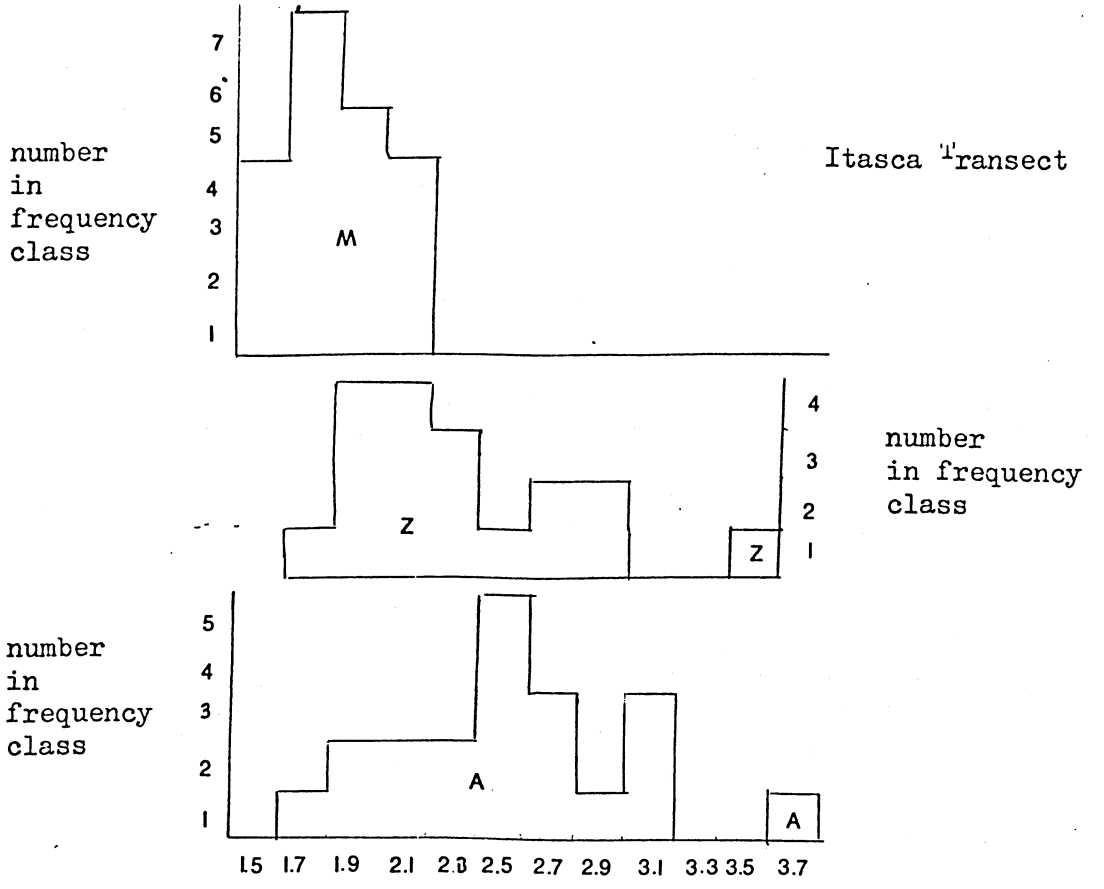
Z = stand Z., distribution of means

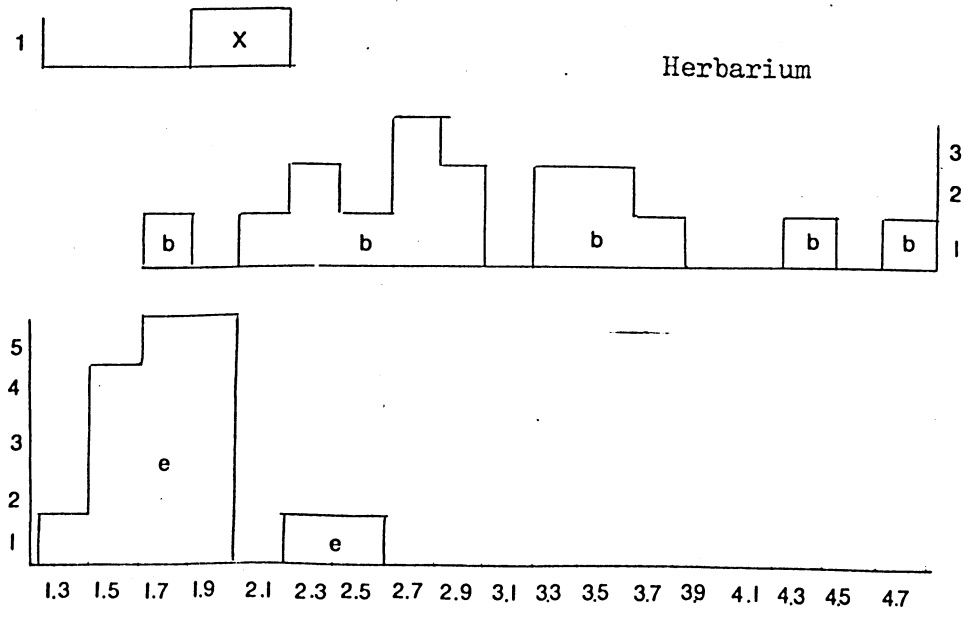
Herbarium

b = trees labeled Quercus borealis, distribution of mean ratios per specimen

e = trees labeled Q. ellipsoidalis, distribution of mean ratios per specimen

x = trees labeled Q. borealis x Q. ellipsoidalis, distribution of mean ratios per specimen


number in frequency class
7
6
5
4
3
2
1
M
Itasca Transect
Z
Z
4
3
2
1
number in frequency class
number in frequency class
5
4
3
2
1
A
A
1.5 1.7 1.9 2.1 2.3 2.5 2.7 2.9 3.1 3.3 3.5 3.7


1
X
Herbarium
b
b
b
b
b
3
2
1
5
4
3
2
1
e
e
1.3 1.5 1.7 1.9 2.1 2.3 2.5 2.7 2.9 3.1 3.3 3.5 3.7 3.9 4.1 4.3 4.5 4.7
ratio of width:depth of acorn cups

Appendix C

Analyses of variance are not valid for the data, as the variances of the populations are not homogeneous (by Bartlett's Test for Homogeneity of Variances and F tests). Non-parametric chi-square tests were applied to the data from the frequency tables for the leaf lobes and leaf indentations and to the acorn-cup ratios. When the hypothesis that the populations of the Itasca transect are homogeneous was rejected it is generally because of stand M. When the same test is applied to stands A and Z alone, the results are not significant.

Acorn cup:

AMZ from contingency tables:

Chi-square = $26.26 > X^2_{.95}(4 \text{ d.f.}) = 9.49$

AZ--$X^2 = 2.36 < X^2_{.95}(3 \text{ d.f.}) = 7.81$

From frequency tables:

	Qb	Qe	int	total
A	15 (8.3)	2 (3.5)	3 (8.3)	20
M	0 (8.3)	4 (3.5)	16 (8.3)	20
Z	9 (7.3)	4 (3.1)	5 (7.3)	18
	24	10	24	58

MZ -- $X^2 = 14.7 > X^2_{.95}(3 \text{ d.f.}) = 7.81$

MA -- $X^2 = 24.6 > X^2_{.95}(3 \text{ d.f.}) = 7.81$

example:

Q. borealis ratio

2.2-4.8

intermediate

2.0-2.2

Q. ellipsoidalis

1.1 - 2.6

leaf lobes (frequency classes--red oak, intermediate, or pin oak).

AMZ--$X^2 = 18.03 > X^2_{.95}(4 \text{ d.f.}) = 9.49$ (significant)

	Qb	i	Qe	total
A	20 (17.3)	0	0 (2.67)	20
M	12 (17.3)	0	8 (2.67)	20
Z	20 (17.3)	0	0 (2.67)	20
	52		8	60

Qb = Quercus borealis

i = intermediate

Qe = Q. ellipsoidalis

AZ--$X^2 = 0 < X^2_{.95}(3 \text{ d.f.}) = 7.81$ (not significant)

MZ (or A) $X^2 = 9.35 > X^2_{.95}(3 \text{ d.f.}) = 7.81$ (significant)

Q. borealis-- 9.1 lobes

intermediate-- 7.7-9.1 lobes

Q. ellipsoidalis-- 7.7 lobes

herbarium red oak vs. pin oak, frequency classes, leaf lobes.

Red, pin $X^2 = 62.94$ $X^2_{.95}(1 \text{d.f.}) = 3.84$ (significant differences between groups)

F (Qb, Qe) = 1.69 $F_{.95}(60, \ ) = 1.4$ (same data tested differently, significant)

leaf indentation (frequency classes--red oak, intermediate, or pin oak).

Q. borealis 66.5%, intermediate 66.5-81.5%,

Q. ellipsoidalis 81.5%

AMZ--$X^2 = 14.90 > X^2_{.95}(4 \text{ d.f.}) = 9.49$ significant, classes are different.

AZ--$X^2 = 1.03 < X^2_{.95}(3 \text{ d.f.}) = 7.81$ not significant

AM--$X^2 = 7.02 < 7.81$ not significant

MZ--$X^2 = 10.0 > 7.81$ significant

Herbarium, red oak vs pin oak, frequency class of leaf indentation $F(Qb, Qe) = 2.702 > F_{.95}(60, \ ) = 1.4$

dbh of oaks--Bartlett's test for homogeneity of variance for pooled data from stands A, M, and Z.

$X^2 = 9.89 > X^2_{.95}$ (2d.f.) = 5.99 significant; therefore variances are not homogeneous and linear regression is not valid.

Basal areas

oaks $X^2 = 1.25 < X^2_{.95}(2d.f.) = 5.99$

point-quarter trees $X^2 = .27 < X^2_{.95}(2d.f.) = 5.99$

Kruskal-Wallis test for the same data

$$\frac{H}{D} = 1.2 < X^2_{.95}(2d.f.) = 5.99$$

There is no difference in basal areas among the groups.

Appendix D

Results of measurements of leaves in U of M herbarium

mean from 3 leaves/sheet

Quercus borealis

	Tree Sheet #	Avg. # lobes	Avg. % indent.	Acorn Cup ratio
(1)	23678	7.33	.63	2.6
(2)	99039	9.33	.54	
(3)	529179	8.33	.63	1.8
(4)	554442	8.00	.57	
(5)	322551	9.00	.67	
(6)	99038	7.67	.82	
(7)	99034	8.33	.71	
(8)	541529	7.67	.68	3.0
(9)	356651	9.00	.72	
(10)	542821	9.00	.51	
(11)	99036	9.33	.50	3.4
(12)	47293	8.33	.55	
(13)	419109	7.67	.55	
(14)	419547	8.00	.54	
(15)	371546	8.33	.77	2.7
(16)	352289	9.67	.71	
(17)	422714	10.33	.64	
(18)	352290	10.33	.77	
(19)	446507	9.00	.53	3.5
(20)	457993	8.33	.64	
(21)	462944	10.67	.59	
(22)	225999	8.33	.52	
(23)	442288	8.33	.70	
(24)	618857	12.67	.47	
(25)	424067	9.33	.58	
(26)	421572	9.00	.63	
(27)	542425	10.33	.61	4.7
(28)	318489	8.67	.73	
(29)	292031	10.00	.68	
(30)	581855	11.67	.62	3.7
(31)	541533	8.67	.66	4.3
(32)	385629	10.33	.67	
(33)	446244	10.67	.46	
(34)	262056	8.67	.41	
(35)	371968	9.67	.76	
(36)	558302	7.67	.67	
(37)	594301	9.67	.64	
(38)	568710	9.67	.63	3.2
(39)	99037	9.33	.56	
(40)	446508	9.00	.70	3.6
(41)	449183	9.33	.63	
(42)	449055	9.37	.68	
(43)	393115	8.67	.54	
(44)	372184	7.00	.66	3.2
(45)	353413	10.00	.71	

	Tree Sheet #	Avg. # lobes	Avg. % indent.	Acorn Cup ratio
(46)	332563	10.33	.67	
(47)	383637	8.00	.72	
(48)	295705	10.00	.62	
(49)	558300	8.00	.75	
(50)	99035	7.00	.71	
	$\bar{x}$	9.06	.63	
	348439	10.00	.73	2.3
	558134	10.67	.75	2.4
	618963	10.33	.74	2.4

Results of measurements of leaves and acorns in U of M herbarium

Q. ellipsoidalis

	Tree Sheet #	Avg. # lobes	Avg. % indent.	Acorn Cup ratio
(1)	351259	7.67	.87	1.7
(2)	98508	8.00	.81	1.9
(3)	98506	9.00	.67	
(4)	98520	7.67	.70	2.3
(5)	351263	9.33	.82	
(6)	98542	8.00	.85	
(7)	98551	8.67	.82	1.5
(8)	306880	9.00	.85	
(9)	226010	6.33	.86	
(10)	602222	8.33	.84	
(11)	583886	7.00	.94	
(12)	616706	7.00	.84	
(13)	98433	7.00	.72	
(14)	98523	7.00	.78	1.9
(15)	98435	7.33	.78	1.8
(16)	419681	7.67	.82	
(17)	421118	5.67	.75	1.4
(18)	421466	7.00	.81	
(19)	421465	7.00	.74	
(20)	293304	7.67	.85	
(21)	381087	8.33	.79	1.5
(22)	359905	8.00	.85	1.9
(23)	373860	7.33	.84	
(24)	364411	6.33	.75	
(25)	381389	8.00	.91	2.5
(26)	371248	8.33	.88	
(27)	412108	7.33	.91	1.9
(28)	98521	7.67	.87	
(29)	98515	7.33	.84	
(30)	226012	8.33	.86	
(31)	358433	8.00	.84	
(32)	225982	9.00	.78	
(33)	226903	7.00	.82	
(34)	98544	7.00	.84	
(35)	262221	7.00	.75	1.6
(36)	98543	8.00	.75	
(37)	351262	7.67	.76	
(38)	351265	8.33	.89	1.4
(39)	443311	7.00	.82	
(40)	351264	7.67	.82	1.9
(41)	351261	9.00	.80	
(42)	371529	8.00	.82	
(43)	371519	8.67	.74	
(44)	367710	9.00	.81	